Integrative & Comparative Biology

Volume 58 Number 1 July 2018

CONTENTS

Awards, Announcements, and Appointments

ICB Perspectives

Science in the Public Eye: Leveraging Partnerships

Organized by Martha Merson, Nick Hristov, & Louise Allen

Sponsored by DAB, DCB, DCE, DEDE, DNNSB & DVM

Errata

OXFORD
UNIVERSITY PRESS

OXFORD OPEN

Integrative & Comparative Biology Volume 58 Number 1 July 2018

OXFORD

ISSN 1540-7063 (PRINT)
ISSN 1557-7023 (ONLINE)

Integrative & Comparative Biology

Volume 58 Number 1 July 2018

academic.oup.com/icb

Integrative and Comparative Biology
academic.oup.com/icb
Society for Integrative and Comparative Biology

Integrative and Comparative Biology (ICB) publishes high-impact, peer-reviewed articles in integrative, comparative and organismal biology. Many papers communicate the proceedings of symposia and other events at the annual meeting of the Society for Integrative and Comparative Biology. However, we also publish forward-looking review, synthesis, perspectives and empirical articles selected by the editorial board. More information about this second category of papers is available at: https://academic.oup.com/icb/pages/direct_submission.

Editor-in-Chief

Lynn B. Martin, University of South Florida

Managing Editor

Suzanne C. Miller

Associate Editors

Anna Ahn, Harvey Mudd College
Ryan Earley, University of Alabama
Cameron K. Ghalambor, Colorado State University
H. Art Woods, University of Montana

Assistant Editors

Divisional Representatives
- **Animal Behavior (DAB)**
  - **Tracy Langkilde** (2021), **Penn State University**
- **Comparative Biomechanics (DCB)**
  - **Tyson Lee Hedrick** (2022), University of North Carolina, Chapel Hill
- **Comparative Endocrinology (DCE)**
  - **Rosemary Knapp** (2023), University of Oklahoma
- **Comparative Physiology & Biochemistry (DCPB)**
  - **Donovan German** (2021), University of California, Irvine
- **Ecoimmunlogy & Disease Ecology (DEDE)**
  - **Ken Field** (2020), Bucknell University
- **Ecology & Evolution (DEE)**
  - **Michael Dillon** (2022), University of Wyoming
- **Evolutionary Development Biology (DEDB)**
  - **David Platchetzki** (2023), University of New Hampshire
- **Invertebrate Zoology (DIZ)**
  - **Bruno Pernet** (2020), California State University
- **Neurobiology (DNB)**
  - **Petra Lenz** (2023), University of Hawaiʻi at Mānoa
- **Phylogenetics and Comparative Biology (DPCB)**
  - **Lars Schmitz** (2019), W.M. Keck Science Department of Claremont McKennae, Pitzer, and Scripps Colleges
- **Vertebrate Morphology (DVM)**
  - **Sharlene Santana** (2021), University of Washington

Assistant Editors (non division representatives):

Manny Azizi (2019), University of California, Irvine
Robert Cox (2022), University of Virginia
David Julian (2019), University of Florida
James Gillooly (2022), University of Florida
Anjali Goswami (2022), University College London
Stephane Hourdez (2020), Centre National pour la Recherche Scientifique Roscoff Marine Laboratory
Brent Sinclair (2022), University of Western Ontario
Ann Tarrant (2019), Woods Hole Oceanographic Institution

Social Media Manager

Isaac Ligocki, University of California, Davis

Executive Officers, Society for Integrative and Comparative Biology

- **President**
  - **Louis Burnett (2019)**
- **President-Elect**
  - **Elizabeth L. Brainerd (2019)**
- **Past President**
  - **Peter Wainwright (2019)**
- **Secretary**
  - **Alice Gibb (2021)**
- **Program Officer**
  - **Susan Williams (2020)**
- **Program Officer Elect**
  - **Richard Blob (2018)**
- **Treasurer**
  - **Karen Martin (2019)**
- **Members-At-Large**
  - **April Hill (2019)**
  - **Creagh Breuner (2020)**
- **Divisional Chairs**
  - **DAB Chair: Jennifer Gumm (2019)**
  - **DCB Chair: Sheila Patek (2019)**
  - **DCE Chair: C. Loren Buck (2020)**
  - **DCPB Chair: Kimberly Hammond (2020)**
  - **DEDB Chair: Kim Hoke (2020)**
  - **DEDE Chair: Travis Wilcoxen (2020)**
  - **DEE Chair: Robert Cox (2019)**
  - **DIZ Chair: Kenneth M. Halanych (2020)**
  - **DNNSB Chair: Michael Baltzley (2020)**
  - **DPCB Chair: Kerin Claeson (2019)**
  - **DVM Chair: John Hutchinson (2019)**
- **Editor-in-Chief, ICB: Lynn B. Martin (2021)**
- **SPDAC Chair: Zen Faulkes (2019)**
- **Ed. Council Chair: Bram Lutton (2021)**
- **BPC Chair: Stacey Combes (2019)**
- **Executive Director: Brett J. Burk**

Cover image: Left: *Joshua tree roots with mycorrhizal fungi soil 3*, acrylic paint, Joshua tree seed oil, alcohol, soap; Right: *Joshua tree roots with mycorrhizal fungi soil 1*, acrylic paint, Joshua tree seed oil, alcohol, soap.
Artist/scientist: Juniper Harrower, juniperharrower.com.

Environmental & Ethical Policies

Oxford Journals is committed to implementing environmentally friendly policies and practices. Where possible we use environmentally accredited papers. Look out for the FSC and SFI logos on our journals.

For more information visit:
academic.oup.com/journals/pages/about_us/ethical_policies

OXFORD
UNIVERSITY PRESS

Integrative and Comparative Biology
Volume 58 Number 1 July 2018
Society for Integrative and Comparative Biology

CONTENTS

Awards, Announcements, and Appointments

ICB Perspectives

Science in the Public Eye: Leveraging Partnerships

Organized by Martha Merson, Nick Hristov, & Louise Allen
Sponsored by DAB, DCB, DCE, DEDE, DNNSB & DVM

Errata

Subscriptions

A subscription to *Integrative and Comparative Biology* comprises 6 issues. Prices include postage; for subscribers outside the Americas, issues are sent air freight. Airmail rates are available on request. Integrative and Comparative Biology Advance Access contains papers that have recently been accepted but have not yet been included within an issue. Advance Access is updated daily.

Annual Subscription Rate (Volume 58, 6 issues, 2018)
Institutional
Print edition and site-wide online access: US$1142/£601/€901
Print edition only: US$1052/£554/€831
Site-wide online access only: US$849/£447/€670

Please note: US$ rates apply in the US and Canada, € in Europe, and UK£ in the UK and Rest of World. Payment for orders to be delivered within Europe (excluding the UK) should be made in euros.

There are other subscription rates available; for a complete listing, please visit academic.oup.com/icb/subscribe.

Full prepayment in the correct currency is required for all orders. Orders are regarded as firm, and payments are not refundable. Subscriptions are accepted and entered on a complete volume basis. Claims cannot be considered more than four months after publication or date of order, whichever is later. All subscriptions in Canada are subject to GST. Subscriptions in the EU may be subject to European VAT. If registered, please supply details to avoid unnecessary charges. For subscriptions that include online versions, a proportion of the subscription price may be subject to UK VAT. Personal rates are applicable only when a subscription is for individual use and are not available if delivery is made to a corporate address.

The current year and two previous years issues are available from Oxford University Press. Previous volumes can be obtained from the Periodicals Service Company, 11 Main Street, Germantown, NY 12526, USA. E-mail: psc@periodicals.com. Tel: (518) 537-4700. Fax: (518) 537-5899. Web: www.periodicals.com/oxford.

Contact information: Journals Customer Service Department, Oxford University Press, Great Clarendon Street, Oxford OX2 6DP, UK. E-mail: jnls.cust.serv@oup.com. Tel: +44 (0)1865 353907. Fax: + 44 (0)1865 353485. **In the Americas, please contact:** Journals Customer Service Department, Oxford University Press, 2001 Evans Road, Cary, NC 27513, USA. E-mail: jnlorders@oup.com. Tel: (800) 852-7323 (toll-free in USA/Canada) or (919) 677-0977. Fax: (919) 677-1714. **In Japan, please contact:** Journals Customer Service Department, Oxford University Press, Tokyo 4-5-10-8F Shiba, Minato-ku, Tokyo 108-8386, Japan. E-mail: custserv.jp@oup.com. Tel: (03) 3813 1461. Fax: (03) 3818 1522.

Methods of payment: (i) Cheque (payable to Oxford University Press, Cashiers Office, Great Clarendon Street, Oxford OX2 6DP, UK) in GB£ Sterling (drawn on a UK bank), US$ Dollars (drawn on a US bank), or EU€ Euros. (ii) Bank transfer to Barclays Bank Plc, Oxford Group Office, Oxford (bank sort code 20-65-18) (UK), overseas only Swift code BARC GB 22 (GB£ Sterling to account no. 70299332, IBAN GB89BARC20651870299332; US$ Dollars to account no. 66014600, IBAN GB27BARC20651866014600; EU€ Euros to account no. 78923655, IBAN GB16BARC20651878923655). (iii) Credit card (Mastercard, Visa, Switch or American Express).

Postal information

Integrative and Comparative Biology (ISSN 1540-7063) is published six times a year, in July, August, September, October, November, and December, by the Society for *Integrative and Comparative Biology*, 1313 Dolley Madison Blvd., Ste. 402, McLean, VA 22101. Periodicals Postage Paid at McLean, VA, and additional mailing offices. Postmaster: send address changes to ICB, Customer Service Department, Oxford Journals, 2001 Evans Road, Cary, NC 27513-2009.

Oxford Journals Environmental and Ethical Policies

Oxford Journals, a division of Oxford University Press, is committed to working with the global community to bring the highest quality research to the widest possible audience. Oxford Journals will protect the environment by implementing environmentally friendly policies and practices wherever possible. Please see academic.oup.com/journals/pages/about_us/ethical_policies for further information on environmental and ethical policies.

Permissions

For information on how to request permissions to reproduce articles or information from this journal, please visit academic.oup.com/journals/pages/access_purchase/rights_and_permissions.

Advertising

Advertising, inserts and artwork enquiries should be addressed to Advertising and Special Sales, Oxford Journals, Oxford University Press, Great Clarendon Street, Oxford, OX2 6DP, UK. Tel: +44 (0)1865354767. Fax: +44 (0)1865 353774. E-mail: jnlsadvertising@oup.com.

Disclaimer

Statements of fact and opinion in the articles in *Integrative and Comparative Biology* are those of the respective authors and contributors and not of *Integrative and Comparative Biology*, the Society for Integrative and Comparative Biology, or Oxford University Press. Neither Oxford University Press, the Society for Integrative and Comparative Biology, nor *Integrative and Comparative Biology* make any representation, express or implied, in respect of the accuracy of the material in this journal and cannot accept any legal responsibility or liability for any errors or omissions that may be made. The reader should make her or his own evaluation as to the appropriateness or otherwise of any experimental technique described.

Integrative and Comparative Biology is printed on acid-free paper that meets the minimum requirements of ANSI Standard Z39.48-1984 (Permanence of Paper).

Oxford University Press is a department of the University of Oxford. It furthers the University's objective of excellence in research, scholarship, and education by publishing worldwide.

Integrative and Comparative Biology is covered by the following major indexing services: Aquatic Sciences and Fisheries Abstracts, Biological Abstracts, Biological and Agricultural Index, Chemical Abstracts, Current Contents, General Science Index, MEDLINE, Science Citation Index, and Zoological Record.

Typeset by Cenveo Publisher Services, Bangalore, India; Printed by Sheridan Press, USA.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 1–2
doi:10.1093/icb/icy030

Society for Integrative and Comparative Biology

Awards, Scholarships, and Grants Awarded at the SICB Meeting in January 2018

BEST STUDENT PRESENTATION AWARD WINNERS 2018

DAB

Oral Presentation	Sydney Hope, Virginia Tech
Oral Presentation	Margaret Tanner, University of Colorado, Denver

DCB

Oral Presentation—Mimi A.R. Koehl and Steven Wainwright Award	Alexis Noel, Georgia Tech
Poster Presentation—Steven Vogel Award	Michelle Graham, Virginia Tech

DCE

Oral Presentation—Aubrey Gorbman Award	Nathaniel Rieger, UW Madison
Poster Presentation—Lynn Riddiford Award	Brenna Gormally, Tufts University

DCPB

Oral Presentation—Louis Guillette Award	Samantha Leigh, University of California Irvine
Poster Presentation—Louis Guillette Award	Pegah Nabili, Lake Forest College

DEDB

Oral Presentation	Allan Carrillo-Baltodano, Clark University
Poster Presentation	Stephanie Neal, University of Florida

DEDE

Oral Presentation	Tosha R. Kelly, University of Western Ontario
Poster Presentation	Ashley C. Love, Oklahoma State University

DEE

Oral Presentation—Raymond Huey Award	Alisha Shah, Colorado State University
Poster Presentation—Raymond Huey Award	Meredith Miles, Wake Forest University

DIZ

Oral Presentation	Elizabeth Clark, Yale University
Poster Presentation	Kelsey Nannini, California State University Fullerton
Wenner Strong Inference Award	Emily Richardson, College of William and Mary

DNNSB

Oral Presentation	Diana Li, Stanford University
Poster Presentation	Teisha King, Louisiana State University

DPCB

Oral Presentation—David and Marvalee Wake Award	Daniel J. Paluh, University of Florida
Poster Presentation—David and Marvalee Wake Award	Madison Sage Wiltse, Pitzer College

DVM

Oral Presentation—D. Dwight Davis Award	Kristin Stover, UC Irvine
Poster Presentation—Karel F. Liem Award	Dylan Wainwright, Harvard University

2018 DOROTHY H. SKINNER AWARD

Awarded to Kirstin Brink, University of British Columbia

2018 GEORGE A. BARTHOLOMEW AWARD

Awarded to Caroline Williams, University of California, Berkeley

2018 M. PATRICIA MORSE AWARD

Awarded to William Hoese, California State University, Fullerton

2018 LIBBIE HYMAN MEMORIAL SCHOLARSHIP

Awarded to Matthew Boot of Ohio State University
Andre LaBuda of California State University, Los Angeles

2018 JOHN A. MOORE LECTURE

Awarded to Katayoun Chamany, Eugene Lang College

2018 HOWARD BERN AWARD

Awarded to David Norris, University of Colorado, Boulder

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 3–5
doi:10.1093/icb/icy031

Society for Integrative and Comparative Biology

Awards, Scholarships, and Grants Awarded at the SICB Meeting in January 2018

FELLOWSHIPS FOR GRADUATE STUDENT TRAVEL (FGST) AWARDS 2018

Levi Storks, The University of Missouri, Columbia
“Behavioral flexibility and its neuronal substrates across urban and forest habitats”

Christian Brown, University of South Florida, Tampa
“Tracking salamanders to track climate change: using PIT telemetry to describe elevational range shifts in *Ambystoma tigrinum nebulosum*”

Joshua Goldberg, University of California, Riverside
“Population size structure as an agent of evolutionary change”

Austin Spence, University of Connecticut
“Will oxygen limit climate-induced range shifts?”

Emily Richardson, The College of William and Mary
“Assessing the causes and prevalence of cloning in larval crown-of-thorns seastars: implications for estimating and modeling dispersal potential”

Anthony Gilbert, Ohio University
“Phenotypic plasticity along an extinction-risk gradient: the synergy of multiple plastic responses in avoiding demographic collapse”

Hayden Davis, Villanova University
“Convergent evolution of *Cyrtodactylus* in Bornean karst formations”

SICB GRANTS IN AID OF RESEARCH (GIAR) 2018

Sarah Amonett, The University of Mississippi
“Maternal antibody transmission against a novel pathogen in Eastern bluebirds”

Ashley Love, Oklahoma State University
“Maternal disease and offspring telomere length”

Alexa Lindauer, The University of Nevada, Reno
“Out of the frying pan, into the fire: does drought-induced tadpole stress exacerbate disease susceptibility post metamorphosis?”

Kimberly Berrier, California State University, Northridge
“Adaptive evolution or preadapted tactics? A genomic approach to identifying the mechanisms underlying invasion success”

Theresa Gunn, Georgia Southern University
“Physiological regulation of stingray color change”

Thomas Boag, Stanford University
"Evaluating the effects of climate change on metabolic habitat loss and competitive exclusion potential between the red abalone (*Haliotis rufescens*) and purple sea urchin (*Strongylocentrotus purpuratus*) along the Central California coastal upwelling zone"

Dina Navon, The University of Massachusetts, Amherst
"Building a bigger fin: recruitment of wnt7aa during cichlid fin development via a novel enhancer"

Linyi Zhang, Rice University
"Why are insects so diverse: testing the repeatability of ecological and genetic divergence across a community of gall wasps"

Sarin Tiatragul, Auburn University
"Fitness consequence of nesting behavior in urban lizards"

Rachel Moran, University of Illinois at Urbana–Champaign
"Using linkage maps to compare chromosomal structure between two diverging species of darters"

Rachel Petersen, New York University
"Mechanisms of cryptic female choice in a non-human primate"

Magalie Valere Rivet, Loma Linda University

"Expression profiles of hypoxia inducible factor (HIF) in the hermit crab *Pagurus samuelis* under hypoxic conditions"

Aaron Griffing, Marquette University
"Differential regenerative ability in New Caledonian geckos (*Correlophus*): an untapped evolutionary model to study tail regeneration"

Shumpei Maruyama, Oregon State University
"The identification of symbiosis-specific proteins in a cnidarian-algal symbiosis using aptamer Cell-SELEX"

Keegan Melstrom, University of Utah
"Quantifying the relationship between diet and dental morphology through the ontogeny of herbivorous squamates"

Leann Louis, University of California, Berkeley
"How does the bone resorption that occurs when a bird is laying an egg influence bone morphology and mechanical properties?"

Grace Capshaw, University of Maryland, College Park
"Exploring extratympanic sound transmission pathways for hearing in 'earless' vertebrates"

Brooke Sykes, University of Mississippi
"Consequences of heat-stress in an altricial songbird"

Sarah Wenner, California State University, Northridge
"Conservation genetics of an emblematic reptile in urban Southern California"

Casey Coomes, The University of Tennessee, Knoxville
"If you can't take the heat: the effects of heat stress on mating behaviors in songbirds"

Alisha Shah, Colorado State University
“Assessing the combined effects of temperature and predation on elevation range limits of temperate and tropical mayflies”

Jessica Cusick, Florida State University
“Investigating proximate causes of interindividual variation in cooperative behavior”

Kelly Robinson, San Diego State University
“Coevolution of venom and venom resistance in rattlesnakes and small mammals”

Emily Powell, University of Miami
“The role of visual mate-recognition signals in the reinforcement of reproductive isolation in the black-spotted least gecko (*Sphaerodactylus nigropunctatus*) complex”

Melissa Ingala, The American Museum of Natural History
“You are more than what you eat: functional contribution of the microbiome to metabolism in frugivorous bats”

Victor Munteanu, Clemson University
“Effects of ecological transitions on locomotor morphology: did changing bone loads facilitate limb elongation in arboreal vertebrates?”

Lisa Treidel, University of California, Berkeley
“The metabolic cost of resource availability fluctuations: does metabolic plasticity during starvation come with the cost of *in vivo* reactive oxygen species (ROS) production?”

Nicole Weigand, Ohio University
“Evaluating potential effects of proximity to roads in a road-naive population of turtles”

Integrative and Comparative Biology
Integrative and Comparative Biology, volume 58, number 1, pp. 6–8
doi:10.1093/icb/icy003
Society for Integrative and Comparative Biology

Announcement of New Assistant Editors 2018

Robert Cox

Robert Cox is an Associate Professor in the Department of Biology at the University of Virginia. His research explores the evolution of differences between males and females by integrating comparative analyses, hormone manipulations, quantitative and molecular genetics, and field studies of natural and sexual selection. Bob received his BA in 1999 from the College of the Holy Cross and his PhD in 2005 from Rutgers University, where he studied the endocrine basis of sexual dimorphism with Henry John-Alder. He conducted postdoctoral research on avian skin physiology with Joe Williams at Ohio State University and on sexual conflict in *Anolis* lizards with Ryan Calsbeek at Dartmouth College before joining the University of Virginia faculty in 2011. Bob is a recipient of the George A. Bartholomew Award, Chair of the SICB Division of Ecology and Evolution, and also serves on the editorial board for *Physiological and Biochemical Zoology*.

Jamie Gillooly

Jamie Gillooly is an Associate Professor of Biology at the University of Florida. His research typically focuses on describing and explaining broad-scale patterns in organismal biology based on principles of energetics. Jamie received his BA in English Literature from the University of Michigan in 1988, and his PhD in Zoology from the University of Wisconsin-Madison in 2000. Before joining the faculty at Florida, he went on complete a postdoctoral fellowship at the University of New Mexico under the guidance of Jim Brown and Eric Charnov. Jamie currently serves on the editorial board of Proceedings of the Royal Society, Physiological Zoology and Biochemistry, and Evolutionary Ecology Research.

Anjali Goswami

Anjali Goswami is a Research Leader in the Department of Life Sciences at the Natural History Museum and an Honorary Professor in the Department of Genetics, Evolution & Environment at University College London. Her research focuses mainly, but not exclusively, on vertebrate evolution and development, especially using 3D morphometric methods to incorporate data from embryos to fossils to test genetic and developmental hypotheses of modularity and morphological diversity and to reconstruct macroevolutionary patterns through deep time. She also conducts palaeontological fieldwork in India and Argentina, focusing on the period surrounding the last mass extinction. She received her BS from the University of Michigan in 1998 and her PhD from the University of Chicago in 2005. After completing a US National Science Foundation international research fellowship at the Natural History Museum, London, she was appointed as a lecturer at the University of Cambridge in 2007, moving to University College London from 2009 to 2017, where she was jointly appointed as Professor of Palaeobiology in the Department of Genetics, Evolution & Environment and the Department of

Earth Sciences. She has previously served on the boards of *PLoS One*, *Palaeontology*, and the *Journal of Vertebrate Paleontology* and is currently an Associate Editor or on the editorial board for *Evolution*, *Evolution Letters*, *Biology Letters*, and *Palaeobiology*.

Rosemary Knapp

Rosemary Knapp is a Professor in the Biology Department at the University of Oklahoma. Her research focuses on the evolution and endocrine mechanisms underlying parental, and especially paternal, behavior, and within-sex variation in reproductive behavior as exemplified by species with male alternative reproductive tactics. She received her BS from Cook College of Rutgers University in 1984, conducting her honors research with Tim Casey, and an MS from the University of Wisconsin in 1987, advised by Jack Hailman. She subsequently served as Assistant Director of Introductory Biology Laboratories at Barnard College, where she also conducted research in neuroendocrinology with Rae Silver. In 1990, she began pursuing her PhD at Arizona State University with Mike Moore. After completing her PhD in 1996, she was a National Institutes of Mental Health postdoctoral fellow in Neurobiology & Behavior at Cornell University with Andrew Bass. In 1998, she became an Assistant Professor at the University of Oklahoma. She has previously served on the boards of the *Proceedings of the Royal Society B Biological Sciences* and *Hormones and Behavior*.

Petra H. Lenz

Petra H. Lenz is a Research Professor at the Pacific Biosciences Research Center at the University of Hawai‘i at Mānoa. She received a BA from the University of California, San Diego in 1976, and her PhD from the University of California Santa Barbara in 1983. She is a physiological ecologist who has worked on the behavior, sensory physiology, and genetic profiling of marine zooplankton. Currently, she is investigating sensorimotor systems of copepods to determine how these organisms detect and integrate mechanosensory information to escape from predators such as larval fishes. In addition, she studies the physiology of post-embryonic diapause in high-latitude copepods focusing on omics signals, predictive of population responsiveness to environmental change. She is a member of the editorial board of the *Journal of Plankton Research*.

David Plachetzki

David Plachetzki is an Assistant Professor in the Department of Molecular, Cell and Biomedical Sciences at the University of New Hampshire. The Plachetzki lab integrates phylogenetics, genomics, and functional data to ask questions on the origins of novel traits in evolution. Current projects include investigations into the origins of the animal senses, the origins of novel cell types in cyclostome craniates, and the origins of novel symbiotic relationships in sponges. Dr. Plachetzki received his PhD from the University of California at Santa Barbara in 2009, where Todd H. Oakley advised him. Following graduate work, Dr. Plachetzki held postdoctoral fellowships with the Center for Population Biology and the Lifesciences Research Foundation/HHMI, both at the University of California at Davis, where he worked with Richard K Grosberg and Artyom Kopp. Dr. Plachetzki joined the University of New Hampshire as faculty in 2014. He is the recipient of the 2012 Research Award in Animal Science, Veterinary Research, and Zoology from BioMed Central Journals and the 2008 Buschbaum Prize for Excellence in Photomicrography from the American Microscopical Society.

Brent Sinclair

Brent Sinclair hails from New Zealand, and did his undergraduate degree and PhD at the University of Otago, working on ecology and physiology of Antarctic and alpine arthropods with Dr. David Wharton. After a year as a climbing bum, he spent three years as a postdoc with Prof. Steven Chown in Stellenbosch, South Africa, where he continued his alpine and Antarctic work, before moving to a postdoc at University of Nevada Las Vegas where Dr. Steve Roberts did his best to turn him into a *Drosophila* functional genomicist. Since 2006, Brent has been at the University of Western Ontario, where he is now a full professor. Brent's current research ranges from molecular physiology to evolutionary biology, almost all related to insects in the cold. He works on applied questions, particularly the overwintering biology of crop and forest pests, as well as the thermal biology of arthropods in the cold. He is proud to report that the students he trains all end up better at this science gig than he is.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 9–24
doi:10.1093/icb/icy005

Society for Integrative and Comparative Biology

INVITED PERSPECTIVES

High Temperature, Oxygen, and Performance: Insights from Reptiles and Amphibians

Eric J. Gangloff[*,‡] and Rory S. Telemeco[1,†]

*Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA; †Department of Biology, California State University Fresno, Fresno, CA 93740, USA

The first two authors contributed equally to this work.

‡Present address: Station d'Ecologie Théorique et Expérimentale du CNRS, 09200 Moulis, France

[1]E-mail: telemeco@csufresno.edu

Synopsis Much recent theoretical and empirical work has sought to describe the physiological mechanisms underlying thermal tolerance in animals. Leading hypotheses can be broadly divided into two categories that primarily differ in organizational scale: 1) high temperature directly reduces the function of subcellular machinery, such as enzymes and cell membranes, or 2) high temperature disrupts system-level interactions, such as mismatches in the supply and demand of oxygen, prior to having any direct negative effect on the subcellular machinery. Nonetheless, a general framework describing the contexts under which either subcellular component or organ system failure limits organisms at high temperatures remains elusive. With this commentary, we leverage decades of research on the physiology of ectothermic tetrapods (amphibians and non-avian reptiles) to address these hypotheses. Available data suggest both mechanisms are important. Thus, we expand previous work and propose the Hierarchical Mechanisms of Thermal Limitation (HMTL) hypothesis, which explains how subcellular and organ system failures interact to limit performance and set tolerance limits at high temperatures. We further integrate this framework with the thermal performance curve paradigm commonly used to predict the effects of thermal environments on performance and fitness. The HMTL framework appears to successfully explain diverse observations in reptiles and amphibians and makes numerous predictions that remain untested. We hope that this framework spurs further research in diverse taxa and facilitates mechanistic forecasts of biological responses to climate change.

Introduction

For most animals, the proximate mechanisms that underlie reduced performance and eventual death at high temperatures, and how such mechanisms might change with ontogeny and context, are uncertain (reviewed in Angilletta 2009; Clark et al. 2013; Pörtner et al. 2017). Such a mechanistic understanding would greatly enhance our ability to predict the effects of realistic high-temperature exposures on individuals or populations, which are difficult to forecast with traditional methods because responses can be highly variable (e.g., Gunderson and Stillman 2015; Seebacher et al. 2015; Kingsolver and Woods 2016; Sheldon and Dillon 2016; Williams et al. 2016). Even so, much progress has been made toward developing mechanistic models that use knowledge of individual physiology to predict the effects of thermal environments on populations, largely inspired by growing concern over the impacts of global climate change (Buckley 2008; Kearney and Porter 2009; Huey et al. 2012; Kearney 2012; Levy et al. 2015; Malishev et al. 2018). Commonly, such models employ empirically-derived thermal performance curves (TPC, Huey and Stevenson 1979, all terms and abbreviations are defined in Box 1) to predict the effects of thermal environments on organisms and populations (e.g. Colwell et al. 2008; Deutsch et al. 2008; Vasseur et al. 2014; Buckley and Huey 2016; Dillon et al. 2016). TPCs describe how performance varies with temperature—typically performance increases with temperature above a critical minimum (CT_{MIN}) until an optimum is reached (T_{OPT}), then rapidly drops to zero at the critical maximum (CT_{MAX}, see Fig. 1 for examples). Pejus (getting worse) temperatures above and below

Advance Access publication May 2, 2018

Box 1 List of terms and abbreviations

ATP	Adenosine triphosphate
active-aerobic T_{CRIT}	Critical temperature where aerobic respiration is maximized for active individuals (i.e., $\dot{V}_{O_2MAX}$ is maximized, °C)
resting-aerobic T_{CRIT}	Critical temperature where aerobic respiration would be maximized for resting individuals, assuming they survive to such high temperatures (i.e., $\dot{V}_{O_2REST}$ is maximized, °C)
subcellular T_{CRIT}	Critical temperature for subcellular function (°C)
CT_{MAX}	Critical thermal maximum (°C)
HMTL	Hierarchical Mechanisms of Thermal Limitation hypothesis
HSP	Heat shock protein
MPMO	Multiple Performances – Multiple Optima hypothesis (sensu Clark et al. 2013)
OCLTT	Oxygen- and Capacity-Limited Thermal Tolerance hypothesis (sensu Pörtner 2002 and Pörtner et al. 2017)
T_{GAPE}	Gaping temperature: Temperature at which animals gape to promote evaporative cooling (°C)
T_{LETHAL}	Lethal temperature: Temperature at which an organism dies under acute exposure (°C)
T_{OPT}	Optimal temperature for performance (°C)
T_{PANT}	Panting temperature: Temperature at which animals pant to promote evaporative cooling (°C)
T_{PEJUS}	Pejus (i.e. getting worse) temperature (°C, sensu Frederich and Pörtner 2000)
TPC	Thermal performance curve (sensu Huey and Stevenson 1979)
PBT	Preferred body temperature (°C)
$P_{CT_{MAX}}$	Oxygen partial pressure below which CT_{MAX} is reduced (kPa) (sensu Ern et al. 2016)
P_{O_2}	Partial pressure of oxygen (kPa)
P_{CO_2}	Partial pressure of carbon dioxide (kPa)
$\dot{V}_{O_2}$	Oxygen consumption rate (generally mL O_2 min^{-1})

T_{OPT} are described by breakpoints in physiological function (e.g., ventilation rate, heart rate, P_{O_2}) indicative of rapid declines in whole-organism performance (T_{PEJUS}, Frederich and Pörtner 2000; Pörtner 2002; Pörtner et al. 2017). Typically, TPCs are estimated under controlled laboratory conditions for a single trait and time, but TPC shape can vary with season, ontogeny, trait, and prior experience in ways that are difficult to predict (Rezende et al. 2014; Telemeco 2014; Kingsolver and Woods 2016; Williams et al. 2016). Thus, using empirically-derived TPCs to predict the effects of natural environments on performance is problematic because it requires extrapolating from the traits or environments originally used to estimate TPCs, thereby ignoring probable context-dependency. A mechanistic understanding of the processes that underlie thermal performance is needed to predict the effects of variable or novel environments on TPC shape, which will greatly improve models relying on TPCs to predict population responses. In particular, knowledge of the mechanisms that result in loss of function at high temperatures is needed to predict the rate at which performance will drop in response to thermal challenge, the capacity for animals to recover from sublethal thermal exposure, and the capacity for thermal tolerance to change via plasticity or evolution (Helmuth et al. 2005; Buckley and Huey 2016; Williams et al. 2016).

Potential mechanisms explaining why animals lose function at high temperatures can be divided into two major categories differing in the level of organization first affected. At lower levels of organization, subcellular components could be critically impaired when animals are exposed to temperatures above the optimum. Subcellular impairment results from either denaturation of key molecules, such as proteins and cell membranes, or reduced efficiency of these molecules to perform their biological functions (reviewed in Hochachka and Somero 2002; Angilletta 2009; Schulte 2015). Impairment of subcellular components would result in the breakdown of higher levels of organization and lead to rapid performance loss. Alternatively, higher-levels of organization, such as organ systems, could be impaired at temperatures below those that directly affect the performance of their subcellular components if high temperatures disrupt subcellular interactions or pathways necessary for organ system function. A recent mechanistic model explaining organ-system impairment at high temperatures is the oxygen and capacity limited thermal tolerance (OCLTT) hypothesis, which proposes that oxygen demand for aerobic metabolism at high temperatures outpaces the ability of the

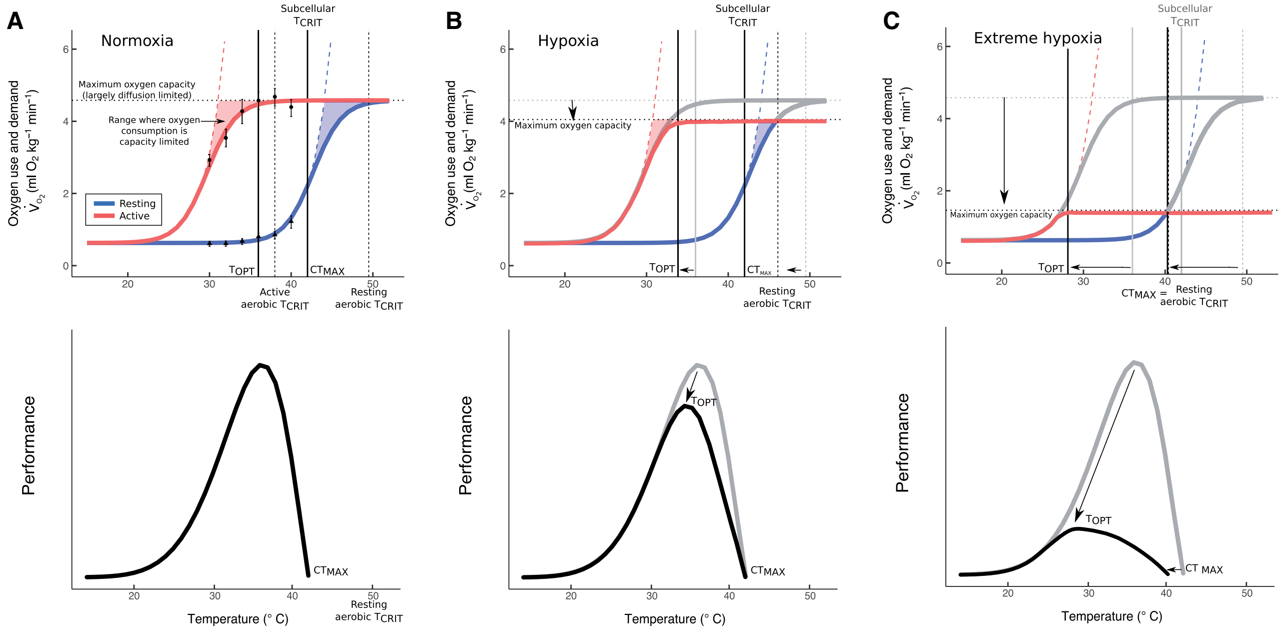


Fig. 1 Schematic of the HMTL framework illustrating proposed relationships between body temperature, oxygen environment, metabolism, thermal limits, and performance. The top row of plots displays resting and active metabolic rates as a function of temperature within thermal and physiological limits, and the bottom row displays predicted thermal performance curves. Panel (**A**) displays these relationships in normoxic environments. Data are means ± s.e.m. for the snake, *P. regius*, from Fobian et al. (2014). These data were used to fit curves for resting and active metabolic rate, which were then used to estimate T_{OPT} (maximal aerobic scope), resting-aerobic T_{CRIT}, active-aerobic T_{CRIT}, and thermal performance curve shape. The critical thermal maximum is 42°C (Fobian et al. 2014). Panel (**B**) Moderate hypoxia (10–20 kPa) is predicted to have no effect on CT_{MAX} or resting metabolism because resting aerobic T_{CRIT} is above subcellular T_{CRIT}. Even so, active-aerobic T_{CRIT} will be reduced thereby lowering aerobic scope, maximal performance, and T_{OPT}. Panel (**C**) Exposure to extreme hypoxia (< 10 kPa) will reduce CT_{MAX} because resting-aerobic T_{CRIT} drops below subcellular T_{CRIT}. Active-aerobic T_{CRIT} will be strongly affected by such hypoxic environments as well, with large reductions in aerobic scope, maximal performance, and T_{OPT}. In Panels B) and C), gray lines illustrate values predicted for normoxia and are included to aid interpretation of changes predicted to result from reduced environmental oxygen availability. Similarly, arrows in Panels B) and C) indicate predicted displacement of maximum oxygen capacity, resting-aerobic T_{CRIT}, T_{OPT}, and CT_{MAX} values given the oxygen environment. Subcellular T_{CRIT} is not predicted to be affected by oxygen environment and therefore is never displaced.

cardiovascular and respiratory systems to provide sufficient amounts of oxygen to tissues (Pörtner 2002; Pörtner and Knust 2007; Verberk et al. 2016; Pörtner et al. 2017). Under this hypothesis, oxygen diffusion and transport capacity limit metabolic rates such that resting rates converge with potential maximum rates at high temperatures thereby reducing aerobic scope to zero (i.e., zero aerobic power budget sensu Pörtner et al. 2017). This mismatch in supply and demand will first reduce aerobic performance at T_{PEJUS} but eventually result in basal oxygen demands not being met and thus collapse of organismal systems at CT_{MAX}. Proponents of OCLTT argue that this mechanism integrates across levels of organization from systemic to molecular mechanisms and can explain diverse evolutionary and ecological phenomena (Pörtner 2002; Pörtner et al. 2017). However, the temporal window, activity range, magnitude, and biological relevancy of reduced aerobic scope at high temperature are debated (Clark et al. 2013; Gräns et al. 2014; Jutfelt et al. 2014; Pörtner 2014; Verberk et al. 2016; Jutfelt et al. 2018). Identifying the level of organization first impaired by high temperature is necessary to understand how temperature affects whole-organism function.

Recent work exploring the mechanisms underlying thermal tolerance in ectotherms focuses on aquatic taxa (e.g., Frederich and Pörtner 2000; Lucassen et al. 2006; Verberk et al. 2013; Gräns et al. 2014; Ern et al. 2016; Pörtner and Gutt 2016; Verberk et al. 2018) and terrestrial arthropods, particularly insects (reviewed in McCue and De Los Santos 2013; Verberk et al. 2016). These observations suggest that subcellular-level mechanisms are more important determinants of thermal tolerance than oxygen capacity limitations in terrestrial taxa, perhaps because oxygen is more abundant in air than in water. However, recent work includes few studies of terrestrial vertebrate ectotherms: non-avian reptiles (hereafter, reptiles) and amphibians. Reptiles and amphibians display varied ecology, life-history, and thermal tolerance (Vitt and Caldwell 2009; Sunday et al. 2011) and are important for a broad understanding of thermal tolerance. Additionally, these animals frequently contend with challenging temperatures, with some species inhabiting the hottest terrestrial environments (Cowles and Bogert 1944; Vitt and Caldwell 2009; Sunday et al. 2014). Moreover, both the thermal and oxygen environment can vary throughout ontogeny (e.g., aquatic to terrestrial transition in amphibians), and modes of respiration can vary (e.g., cutaneous respiration in many amphibians and some reptiles, such as turtles; Hutchison et al. 1968; Glass et al. 1981; Wang 2011). Because of these traits, reptiles and amphibians have been important models for thermal physiology and ecology for the last century (e.g., Cowles and Bogert 1944; Snyder and Weathers 1975; Huey and Stevenson 1979; Huey 1982; Huey and Berrigan 2001; Vitt and Caldwell 2009; Kearney 2012). This historic work can be leveraged to address modern ideas, such as the OCLTT hypothesis. Furthermore, these taxa are at risk of high-temperature induced extinction resulting from global climate change (Thomas et al. 2004; Huey et al. 2010; Rohr and Raffel 2010; Sinervo et al. 2010; Kearney 2013). Here, we apply the rich history of physiological studies in reptiles and amphibians to modern hypotheses for mechanisms underlying thermal performance and tolerance. This will complete taxonomic coverage of recent reviews, and, more importantly, further understanding of how organismal performance and survival are restricted by high temperatures.

In this commentary, we begin by synthesizing evidence for subcellular- and organ-system-level failures underlying high temperature tolerance and performance in reptiles and amphibians. Because neither framework satisfactorily explains observed patterns individually, we next build upon work in other taxa to present an integrative framework combining both subcellular and organ-system sensitivity to high temperatures and the thermal performance curve paradigm. Using data for reptiles and amphibians, we illustrate how this combined framework appears to predict a broad array of physiological and behavioral observations. We conclude by identifying future research directions to test this framework and discuss how it might be applied to other systems to predict consequences of future high-temperature exposure for organisms and populations.

Evidence for mechanisms underlying thermal tolerance and performance in reptiles and amphibians

Subcellular mechanisms

High temperatures compromise the structure and function of subcellular components, such as enzymes and cell membranes (Fields 2001; Hochachka and Somero 2002) but such damage will only underlie organismal thermal tolerance if it occurs at temperatures below those affecting function at higher levels of organization, such as organ systems (Pörtner 2002). The complexities of enzymatic interactions make extending observations for individual reactions to the whole cell or organism potentially problematic (Schulte 2015). Nonetheless, the observation that subcellular components are frequently stable to temperatures above the critical and lethal limits of animals (hereafter, CT_{MAX} and T_{LETHAL}), commonly maintaining function to temperatures >50°C and capable of evolving stability to 120°C (Fields 2001), was an important motivation for the development of hypotheses such as OCLTT (Pörtner 2001; 2002; Pörtner et al. 2017). For example, CT_{MAX} in reptiles and amphibians generally ranges from mid-30s to low 40s °C (Brattstrom 1965; Sunday et al. 2011, 2014), although a few warm-adapted reptiles tolerate acute exposure to 47.5°C such as the desert iguana (*Dipsosaurus dorsalis*) (Cowles and Bogert 1944; Brattstrom 1965). Even so, most reptile and amphibian proteins do not lose function until they experience temperatures well above CT_{MAX}. For example, ribonucleases from three frog species were stable up to 85°C and maintained high activity at temperatures >50°C (Irie et al. 1998), lactate dehydrogenase in *Agama stellio* lizards maintained both stability and function up to 70°C (Al-Jassabi 2002), and alkaline phosphatase maintained high function up to 50°C in four lizard species (Licht 1964). Similarly, acute exposure to CT_{MAX} did not cause tissue damage or reduce function of serum glutamic-oxaloacetic or glutamic-pyruvic transaminases in Great Plains toads (*Anaxyrus cognatus*, Paulson and Hutchinson 1987) and 2.5-h exposure to temperatures just below CT_{MAX} had no effect on mitochondrial respiration or free-radical production in alligator lizards (*Elgaria coerulea* and *E. multicarinata*; Telemeco et al. 2017), implying no subcellular damage. That said, only one key component needs to lose function for the entire organism to become compromised. For example, the activity of myosin ATPase, a key enzyme for organismal muscle function, closely resembled whole-organism thermal performance curves and denatured at relatively low temperatures in eight lizard species corresponding closely to their respective CT_{MAX} (20% denatured between 37°C and 45.2°C; Licht 1964). Subcellular components such as ATPase could underlie thermal tolerance even though most components maintain function to higher temperature.

Given the complexities of subcellular interactions and the paucity of data for the thermal performance of subcellular components in reptiles and amphibians, heat shock protein (HSP) production might better indicate whether subcellular-level components are challenged at sub-critical high temperatures. HSPs commonly act as molecular chaperones, maintaining protein structure and preventing aggregations of denatured proteins, and inducible variants are produced in response to cellular stress or damage (Fernando and Heikkila 2000; Kregel 2002; Daugaard et al. 2007). In diverse reptiles and amphibians, HSPs (particularly HSPA family members) are produced in response to sub-critical high temperatures, and production of HSPs can allow acclimation for increased thermal tolerance (Ulmasov et al. 1992; Fernando and Heikkila 2000; Zatespina et al. 2000; McMillan et al. 2011; Gao et al. 2014; Simoniello et al. 2016; Tedeschi et al. 2016). Moreover, patterns of HSP expression are correlated with thermal tolerance in lizards: warm-adapted species display higher constitutive HSP concentrations, and both initiate and maintain synthesis of HSPs to higher temperatures than more cold-adapted species (Ulmasov et al. 1992; Zatespina et al. 2000). This pattern of increased HSP production correlating with increases in thermal tolerance in reptiles and amphibians, along with observations for myosin ATPase in lizards, provides compelling evidence for subcellular-function loss playing a role in setting thermal limits, despite other subcellular components displaying little loss of function at relevant temperatures.

Organ-system mechanisms

Even though subcellular-level traits will be compromised at sufficiently high temperatures, higher-order systems might break down at lower temperatures and thus be proximally responsible for setting thermal tolerances (Pörtner 2001; 2002; Storch et al. 2014, but see Clark et al. 2013). The OCLTT hypothesis proposes that the highest organizational level in animals is the integrated cardiovascular and respiratory system because all tissues will be limited by their ability to acquire oxygen for respiration, and that this system is compromised by high temperatures prior to other systems (Pörtner 2001; 2002; Storch et al. 2014). However, similar to other terrestrial species (Klok et al. 2004; McCue and De Los Santos 2013; Verberk et al. 2016) and many fish (Clark et al. 2013; Gräns et al. 2014; Norin et al. 2014; Wang et al. 2014; Ern et al. 2016), evidence for the OCLTT mechanism underlying thermal tolerance in reptiles and amphibians is limited. Under the OCLTT hypothesis, maximal and resting rates of oxygen consumption are expected to converge as animals reach their physiological limits at high temperatures, thereby reducing aerobic scope and potentially inducing a short-term reliance on anaerobic respiration (Frederich and Pörtner 2000; Pörtner and Knust 2007; Elaison et al. 2011; Verberk et al. 2013, 2016; Table 1). Some evidence points to such a mechanism playing an important role in early animal evolution, notably in the transition to air breathing (Berner et al. 2007; Giomi et al. 2014; Teague et al. 2017). However, the few studies exposing animals to high temperatures and measuring indicators of aerobic and anaerobic respiration fail to find evidence for oxygen limitation in adult reptiles and amphibians (Carey 1979; Overgaard et al. 2012; Fobian et al. 2014; Gangloff et al. 2016; Telemeco et al. 2017). For example, oxygen consumption ($\dot{V}_{O_2}$) by pythons (*Python regius*) did not plateau at temperatures approaching CT_{MAX} either when at rest or during periods of high metabolic demand (Fobian et al. 2014, Fig. 1), and resting oxygen consumption in garter snakes (*Thamnophis elegans*) increased with temperature with no apparent limit when animals experienced near-lethal temperatures (Gangloff et al. 2016). Moreover, neither garter snakes (*T. elegans*) nor alligator lizards (*E. coerulea* and *E. multicarinata*) transitioned to anaerobic respiration when exposed to near-critical temperatures (Gangloff et al. 2016; Telemeco et al. 2017), despite snakes and lizards rapidly transitioning when oxygen availability is limited during exercise (reviewed in Gleeson 1991). Observations in amphibians are similar to those for reptiles. For example, oxygen consumption, arterial oxygen saturation, and the proportion of saturated hemoglobin did not plateau at high temperatures in active or resting cane toads (*Rhinella marina*), thus providing evidence for these toads' ability to maintain a positive aerobic power budget at near-critical temperatures (Seebacher and Franklin 2011; Overgaard et al. 2012; Winwood-Smith et al. 2015). In both the boreal toad (*Anaxyrus boreas*) and leopard frog (*Lithobates pipiens*), aerobic scope increased with temperature up to 30°C (Carey 1979). Whole-organism lactate concentration also increased with temperature, but there is no indication that either species becomes oxygen limited up to at least 30°C (Carey 1979). These results are in line with previous work showing that amphibians can maintain substantial aerobic scope at temperatures above active and preferred temperatures, although not necessarily at temperatures approaching T_{LETHAL} (Whitford 1973). While such studies provide strong evidence for adult reptiles and amphibians maintaining aerobic scope at high temperatures, we currently lack data on tissue and cellular oxygen supply, such as

Table 1 Experimental designs for testing aspects of the HMTL hypothesis in reptiles and amphibians with example studies

Experiment type: Factor manipulated	Manipulation	Dependent variable	What it demonstrates	Examples
Temperature	Temperature treatments or ramp in lab	Oxygen capacity parameters ($\dot{V}_{O_2}$, Active $\dot{V}_{O_2}$, alveolar/arterial P_{O_2}, heart rate), lactate production	Maintenance of aerobic scope at high temperatures; No evidence of transition to anaerobic respiration	Carey (1979), Seebacher and Franklin (2011), Overgaard et al. (2012), Fobian et al. (2014), Gangloff et al. (2016)
	Temperature treatments in lab	Skeletal muscle metabolome, mitochondrial function	No transition from aerobic to anaerobic metabolism or subcellular damage at high temperatures	Telemeco et al. (2017)
	Ex vivo temperature treatments	Enzyme activity	Temperature where subcellular components lose function	Licht (1964), Paulson and Hutchinson (1987), Irie et al. (1998), Al-Jassabi (2002)
	Temperature treatments in lab	HSP induction	Temperature that induces a subcellular-protection response	Ulmasov et al. (1992), Fernando and Heikkila (2000), Zatespina et al. (2000), McMillan et al. (2011), Gao et al. (2014), Simoniello et al. (2016), Tedeschi et al. (2016)
Ambient oxygen	Oxygen treatments in lab	Oxygen capacity parameters ($\dot{V}_{O_2}$, heart rate, alveolar/arterial P_{O_2}, ventilation rate)	Aerobic capacity is maintained under conditions of mild hypoxia, but is limited under extreme hypoxia	Boyer (1963, 1966), Withers and Hillman (1983), Pörtner et al. (1991), Branco et al. (1993), Wang et al. (1994)
	Oxygen treatments in lab	PBT	PBT is unaffected by mild hypoxia, but is reduced under extreme hypoxia	Hicks and Wood (1985), Branco et al. (1993), Cadena and Tattersall (2009)
Both ambient oxygen levels and temperature	Temperature and oxygen treatments in lab	Embryo development and survival	Hyperoxia increases survivorship while hypoxia reduces survivorship at high temperatures; Hypoxia reduces development, growth, and hatchling performance at high temperatures	Flewelling and Parker (2015), Liang et al. (2015), Smith et al. (2015)
	Temperature gradient and/or ramp and oxygen treatments in lab	CT_{MAX}, T_{GAPE}, T_{PANT}	Behavioral responses to high temperatures depend on ambient O_2, but only under extreme hypoxia	Dupre et al. (1986), Tattersall and Gerlach (2005), Shea et al. (2016)
	Transplant across altitudinal gradients within species' ranges; Manipulation of ambient O_2 in field; Temperature ramp	CT_{MAX}, T_{GAPE}, T_{PANT}	Behavioral responses to high temperatures depend on ambient O_2, but only under extreme hypoxia	DuBois et al. (2017)
Oxygen capacity	Hematocrit reduction	PBT	Reduced oxygen capacity affects temperature perception and animals choose lower temperatures	Wood (1990), Hicks and Wood (1985)
	Blood volume reduction	Oxygen capacity parameters (heart rate, alveolar/arterial P_{O_2}, ventilation rate)	Heart rate increases while ventilation rate is unchanged by reduced oxygen carrying capacity	Wang et al. (1994)
Observational	–	Quantification of CT_{MAX} across life stages	Oxygen capacity limits thermal tolerance at some developmental stages in larval anurans	Cupp (1980), Sherman (1980), Floyd (1983)
	–	Comparison of PBT, resting $\dot{V}_{O_2}$, Active $\dot{V}_{O_2}$,	PBT matches temperature of maximal aerobic scope in lizards	Wilson (1974)

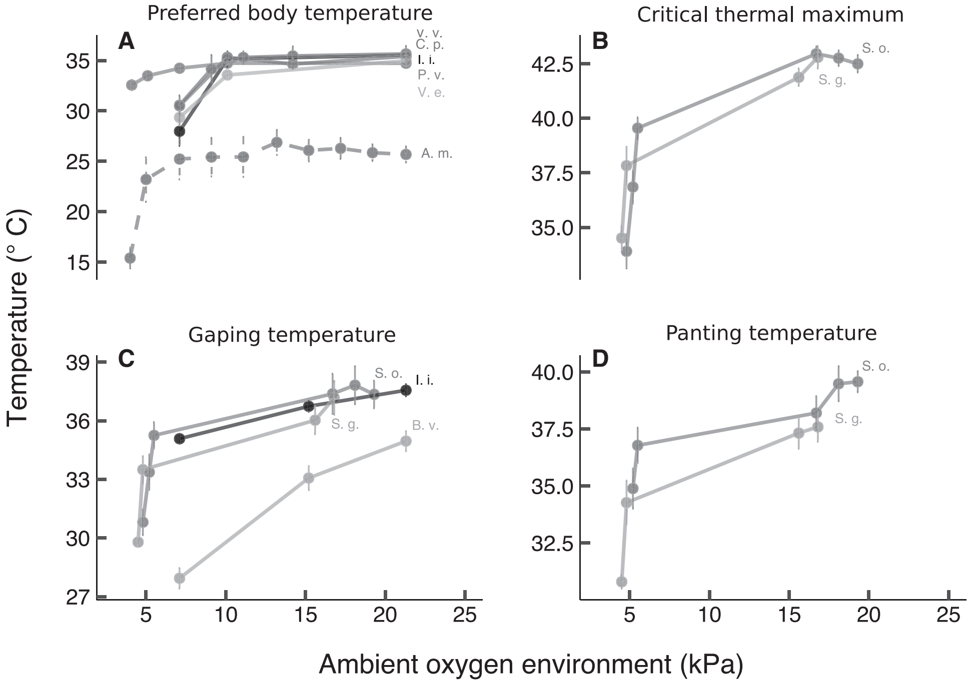


Fig. 2 Thermal preference and tolerance are unaffected by moderate hypoxia but reduced in extremely hypoxic environments (<10 kPa). This "broken-stick" pattern is apparent for (**A**) PBT (i.e. behavioral anapyrexia), (**B**) critical thermal maximum, (**C**) gaping temperature, and (**D**) panting temperature across species. Data are mostly available for lizards (solid lines) but PBT data are also available for alligator (dashed line). Lines between points are included to aid visualization, but connections between values at normoxia and hypoxia are likely nonlinear. Colors (online only) and initials denote species: A.m., *Alligator mississippiensis*; B.v., *Basiliscus vittatus*; C.p., *Ctenosaura pectinata*; I.i., *Iguana iguana*; P.v., *Pogona vitticeps*; S.g., *Sceloporus graciosus*; S.o., *Sceloporus occidentalis*; V.e., *Varanus exanthematicus*; V.v., *Varanus varius*. Data are means ± s.e.m. derived from the literature. See Supplementary Table S1 for data and citations.

venous P_{O_2}, which would more directly test the mechanisms described by the OCLTT hypothesis (Pörtner et al. 2017, 2018).

A second approach for testing the influence of oxygen capacity on thermal constraints is to manipulate oxygen availability and examine changes in thermal behavior or tolerance (Table 1). Under the OCLTT hypothesis, hypoxia is predicted to reduce thermal optima and tolerance limits (Smith et al. 2015; Verberk et al. 2016; DuBois et al. 2017), and this prediction is somewhat supported in reptiles and amphibians. For example, CT_{MAX}, preferred body temperature (PBT), panting temperature (T_{PANT}), and gaping temperature (T_{GAPE}) are reduced when diverse species are exposed to very-low oxygen environments (<10 kPa; mostly lizards examined; Hicks and Wood 1985; Dupre et al. 1986; Branco et al. 1993; Cadena and Tattersall 2009; Shea et al. 2016; DuBois et al. 2017; Fig. 2) and when hematocrit is experimentally reduced (only PBT examined; Hicks and Wood 1985; Wood 1990). Hypoxia-induced PBT reduction is a well-described phenomenon in ectotherms, termed "behavioral anapyrexia," that allows adaptive reduction of metabolic demand when oxygen is limited (Hicks and Wood 1985; Wood and Gonzales 1996; Steiner and Branco 2002; Hicks and Wang 2004), supporting the hypothesis that oxygen limitation influences thermal preference and possibly tolerance. Along with CT_{MAX}, reductions in T_{GAPE} and T_{PANT}, which provide an indication of perceived heat stress (Heatwole et al. 1973; Tattersall et al. 2006; DuBois et al. 2017), imply reduced thermal tolerance under hypoxia. Hypoxia also induces elevated heart rates and reduces both resting and active oxygen consumption ($\dot{V}_{O_2}$) in diverse species (Fig. 3), suggesting observed shifts in thermal tolerance and behavior are related to physiological limits of oxygen capacity (including diffusion and transport). Interestingly, only extreme hypoxia had the predicted effects on thermal tolerance and behavior, with levels of hypoxia within the range generally found in terrestrial environments having no effect (Figs. 2 and 3). Thus, it is not clear that the OCLTT mechanism will be generally relevant in nature.

In contrast to adult stages, naturalistic hypoxia reduces thermal performance and tolerance in eggs and larvae of reptiles and amphibians. Because

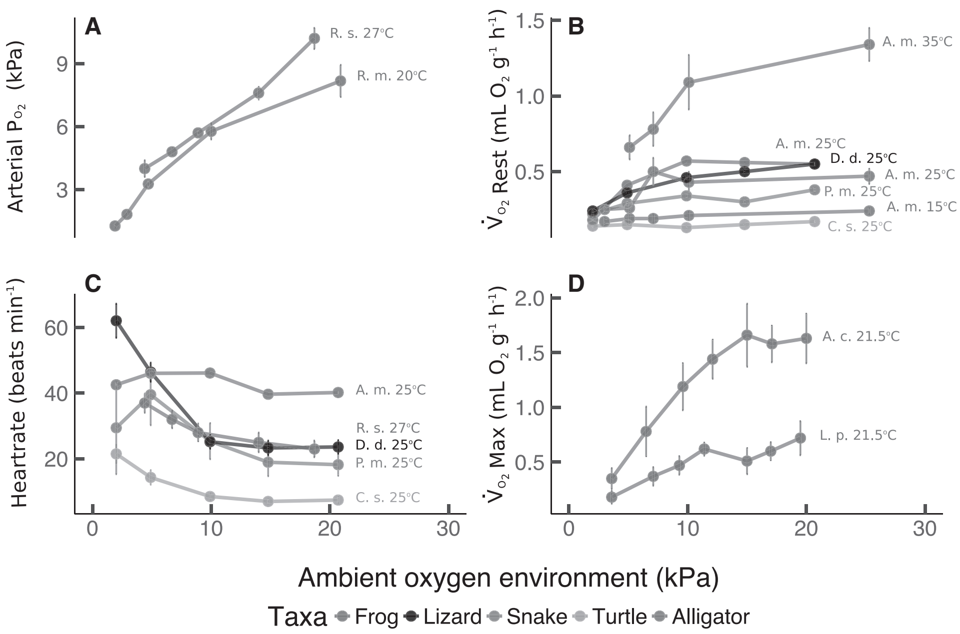


Fig. 3 As the environment becomes increasingly hypoxic, (**A**) arterial P_{O_2} decreases, whereas (**B**) resting metabolic rate, (**C**) heart rate, and (**D**) maximal metabolic rate are relatively unaffected until the environment becomes extremely hypoxic (<10 kPa), similar to thermal preference and tolerance (see Fig. 2 for comparison). Colors (online only) denote taxonomic group whereas initials denote species: A.c., *Anaxyrus cognatus* (formerly *Bufo cognatus*); A.m., *Alligator mississippiensis*; C.s., *Chelydra serpentina*; D.d, *Dipsosaurus dorsalis*; L.p., *Lithobates pipiens* (formerly *Rana pipiens*); P.m., *Pituophis melanoleucus*; R.m., *Rhinella marina* (formerly *Bufo marinus*); R.s., *Rhinella schneideri* (formerly *Bufo paracnemis*). A.c., L.p., R.s., and R.m. are frogs, D.d. is a lizard, P.m. is a snake, C.s. is a turtle, and A.m. is an alligator. Experimental temperature is given to the right of the species' initials. Data are means ± s.e.m. derived from the literature. See Supplementary Table S1 for data and citations.

amphibian eggs and larvae inhabit aqueous environments, environmental oxygen availability is reduced relative to terrestrial stages, thereby increasing the potential importance of the OCLTT mechanism similar to some fully aquatic ectotherms (e.g., Pörtner and Knust 2007; Verberk et al. 2013; Pörtner and Gutt 2016). Oxygen limitation is further exacerbated when species develop in small water bodies that can rapidly lose dissolved oxygen, such as ephemeral pools (Seymour and Bradford 1995; Sacerdote and King 2009), and because amphibian eggs are commonly produced within large gelatinous masses with low oxygen diffusion potential (Pinder and Friet 1994; Woods 1999; Sacerdote and King 2009). Although data are limited, these constraints appear to affect early stage amphibians congruent with oxygen limiting thermal tolerances. For example, amphibians that nest in warm water produce smaller eggs and egg masses to facilitate oxygen diffusion to embryos (Woods 1999; Sacerdote and King 2009), and aquatic larvae born into warm water (from aquatic or terrestrial eggs) are smaller and have lower metabolic demands (Kuramoto 1975; Rollinson and Rowe 2018). In oviparous reptiles, embryonic gas exchange occurs via passive diffusion across the shell into the chorioallantoic membrane, which is much less efficient than adult respiration (Vitt and Caldwell 2009). As predicted by the OCLTT hypothesis, thermal tolerance is reduced when developing embryos experience modest to extreme hypoxia (Flewelling and Parker 2015; Liang et al. 2015; Smith et al. 2015). For example, lower environmental P_{O_2} experienced at high elevations reduces T_{LETHAL} in plateau fence lizard (*Sceloporus tristichus*) embryos compared to P_{O_2} at sea level (Smith et al. 2015), although such modest hypoxia does not affect the thermal tolerance of adult congeners (*S. occidentalis* and *S. graciosus*; Shea et al. 2016; DuBois et al. 2017). Thus, available data suggest that reptiles and amphibians experience ontogenetic shifts in the proximate mechanism underlying thermal tolerance: early stages appear more affected by organ-system-level failures, such as the OCLTT mechanism, whereas later stages are more impacted by subcellular mechanisms.

An integrative framework: HMTL

Available evidence implies that neither failure of subcellular components nor oxygen and capacity limitation are solely responsible for loss of performance at high temperatures in reptiles and amphibians. Rather, mechanisms across levels of organization appear to play partial, context-dependent roles. We propose a unified framework that combines subcellular mechanisms, the oxygen and capacity limited thermal tolerance (OCLTT) hypothesis, and the thermal performance curve (TPC) paradigm. We call this integrative framework "Hierarchical Mechanisms of Thermal Limitation" (HMTL, Fig. 1). Like the OCLTT hypothesis, we propose that oxygen diffusion and transport capacity largely shape thermal performance at sub-critical temperatures via effects of temperature on aerobic scope. However, the HMTL framework explicitly recognizes the importance of subcellular-level mechanisms and allows them to underlie absolute thermal limits, such as CT_{MAX} and T_{LETHAL}. Under this hypothesis, the relative importance of subcellular- and organ-system-level mechanisms on thermal tolerance is context dependent, but predictable. We propose that the HMTL framework explains diverse empirical results and can bring together decades of physiological studies in reptiles and amphibians.

Given that numerous models of thermal performance and tolerance have been proposed, we think that it is useful to state their similarities and differences with HMTL. The HMTL framework builds upon ideas developed for the OCLTT hypothesis proposed by Pörtner and colleagues (recently reviewed in Pörtner et al. 2017) and is similar to that put forth by Ern et al. (2016) for fishes (see Fig. 1 in Ern et al. 2016), but more formally incorporates the TPC paradigm and explicitly describes mechanism-dependent critical temperatures. Importantly, this hypothesis predicts conditions under which subcellular and organ-system failure will set thermal tolerance limits and when transitions are likely to occur. Our framework also differs importantly from the Multiple Performances—Multiple Optima (MPMO) framework put forth by Clark et al. (2013) for fishes. The MPMO suggests a single thermal limit set by an undefined mechanism but multiple, trait-specific optima that can dramatically differ from the temperature that maximizes aerobic scope (summarized in Fig. 7 of Clark et al. 2013). By contrast, we propose multiple potential mechanisms of thermal limitation but a single whole-organism thermal optimum for performance correlated with the temperature that maximizes aerobic scope (although this will be an integration across traits).

Figure 1 illustrates the HMTL framework. In the top row of panels, solid blue and red lines represent the effect of temperature on oxygen consumption during rest and activity, respectively. Assuming activity is maximal, aerobic scope is the difference between these lines. To illustrate this concept with empirical data, we derived these lines by fitting a generalized logistic function to data from Fobian et al. (2014) for pythons (*P. regius*) assuming the shape of the response curve is the same during rest and activity. Based on available data, the general shape of these curves is qualitatively similar across diverse taxa (e.g., Carey 1979; Frederich and Pörtner 2000; Overgaard 2012; Fobian et al. 2014; Ern et al. 2016) and we think that the predictions of the HMTL framework can be generalized beyond the specific data used to generate this illustration. The dotted blue and red lines depict exponential functions fit to these data and illustrate predicted oxygen demand/use if organisms were unconstrained by capacity limitations. The columns illustrate predicted effects of variable oxygen environments, and the bottom row displays TPCs predicted to result given relationships in the top row.

A central assumption of the HMTL framework is that critical thermal limits exist for both subcellular mechanisms (subcellular T_{CRIT}) and aerobic respiration (aerobic T_{CRIT}), and that organismal thermal limits are proximally caused by the lower T_{CRIT} (Fig. 1). The environment and oxygen-handling capacity of the organism will co-determine the hierarchy of these critical limits and thus their relative importance. The subcellular T_{CRIT} is the temperature at which key subcellular components begin to lose function, and should be insensitive to activity state or oxygen environment. By contrast, aerobic T_{CRIT} is the temperature at which oxygen capacity is maximized, and is affected by activity state and oxygen environment. For example, aerobic T_{CRIT} during rest will be higher than aerobic T_{CRIT} during activity because elevated O_2 demand during activity causes capacity limits to be reached more readily (Fig. 1). Moreover, both active- and resting-aerobic T_{CRIT} should be reduced during exposure to hypoxic environments (Fig. 1B, C). Any reduction in environmental oxygen availability below normoxia will reduce aerobic scope. However, CT_{MAX} will only be reduced if environmental hypoxia is sufficient to cause resting-aerobic T_{CRIT} to drop below subcellular T_{CRIT} (Fig. 1C). The environmental oxygen tension where resting-aerobic T_{CRIT} equals subcellular T_{CRIT} is $P_{CT_{MAX}}$ as defined by Ern et al. (2016).

By integrating T_{CRIT} values and aerobic scope, we can derive whole-organism TPCs (Fig. 1, bottom row). Because the active-aerobic T_{CRIT} is the lowest temperature where maximal metabolic rate can be achieved, it closely corresponds to the optimal temperature for aerobic performance (whole-organism T_{OPT}) where aerobic scope is maximized. At temperatures below active-aerobic T_{CRIT}, we predict that performance increases with temperature proportional to aerobic scope. At temperatures above active-aerobic T_{CRIT}, performance will drop until CT_{MAX} is reached, but we predict that the shape of this drop will depend on which T_{CRIT} underlies CT_{MAX}. If resting-aerobic T_{CRIT} underlies CT_{MAX}, the TPC should be more symmetrical with performance and aerobic scope decreasing at a rate mirroring the increase (Fig. 1C). However, if subcellular T_{CRIT} underlies CT_{MAX}, the curve will be asymmetric with loss of performance occurring more rapidly the closer active-aerobic T_{CRIT} is to subcellular T_{CRIT} (Fig. 1A, B).

Assumptions, predictions, and evidence for HMTL in reptiles and amphibians

The HMTL framework produces numerous testable predictions, some of which can be addressed with available data, while others offer exciting avenues for future research. First, any environmental or organismal characteristics that reduce oxygen availability or capacity for oxygen utilization (e.g., aquatic respiration, reliance on cutaneous gas exchange, or life-stages such as eggs with reduced diffusion potential) should increase the probability of resting-aerobic T_{CRIT} underlying CT_{MAX}. This can explain oxygen capacity setting thermal limits in embryos (Smith et al. 2015) but not adults (Overgaard et al. 2012; Fobian et al. 2014; DuBois et al. 2017). Moreover, the transition between aerobic and subcellular T_{CRIT} predicted by HMTL explains extreme experimental hypoxia reducing thermal tolerance in adult reptiles and amphibians, while moderate hypoxia does not (Fig. 1C and Fig. 2B,D). Similarly, HMTL predicts that CT_{MAX} is lower when governed by oxygen limitation than when governed by subcellular mechanisms. Supporting this prediction, CT_{MAX} drops in tadpoles as oxygen demand increases with growth and when respiratory structures are compromised in late-stage metamorphs, but frequently elevates again in terrestrial adults presumably as a result of increased oxygen capacity (Cupp 1980; Sherman 1980; Floyd 1983).

Another important prediction of the HMTL hypothesis is that performance can be limited by oxygen exchange capacity at high temperatures even when CT_{MAX} and T_{LETHAL} are proximally set by subcellular mechanisms. Some interpretations of the OCLTT hypothesis similarly highlight limits on performance at pejus rather than critical temperatures (Pörtner and Knust 2007; Pörtner 2014; Verberk et al. 2016; Pörtner et al. 2017), but other workers suggest OCLTT should explain critical limits to be useful (i.e., Fobian et al. 2014; Smith et al. 2015; Ern et al. 2016; Verberk et al. 2016; DuBois et al. 2017). Under the HMTL framework, activity state is assumed to have no appreciable effect on oxygen capacity, although this may not hold in some highly aerobic taxa (e.g., Wang and Hicks 2004). The extent to which activity-induced increases in oxygen capacity affect thermal performance curves and limits is an important direction for future work. Generally however, individuals in metabolically-demanding states are expected to reach capacity limits at temperatures below those at which such limits are reached by resting individuals. Anaerobic respiration might compensate for short-term mismatches between energy demand and oxygen capacity (reviewed in Gleeson 1991; Fig. 1A, red shaded region), but aerobic constraints are predicted to reduce performance during long-term activity (e.g., digestion, reproduction, recovery; Jackson 2007; Pörtner et al. 2017).

In diverse species, active metabolic rate asymptotes despite increases in cardiovascular output, implying oxygen flux becomes limited at temperatures above active-aerobic T_{CRIT} (e.g., Bartholomew and Tucker 1963; Bennett and Licht 1972; Wilson 1974; Overgaard et al. 2012; Fobian et al. 2014). Furthermore, pulmonary diffusion capacity is limited by reduced plasma gas solubility and hemoglobin binding affinity at high temperatures (Wood and Moberly 1970; Kinney et al. 1977; Pough 1980; Jackson 2007; da Silva et al. 2013). Diffusion limitation of cutaneous gas exchange is also well established (reviewed in Burggren 1988; Wang 2011) and will be important in species that spend considerable time submerged (e.g. Ultsch 1973) or are lungless (e.g., Plethodontid salamanders; Whitford and Hutchison 1965; Spotilla 1972). Finally, increases in the products of anaerobic respiration, such as lactic acid, can lead to blood acidification and thereby further declines in blood oxygen affinity (Bennett 1973). The interaction of numerous factors at high temperatures reduces oxygen capacity, which in turn limits aerobic performance at high temperatures in reptiles and amphibians, regardless of the mechanism governing CT_{MAX} (further reviewed in Jackson 2007).

The HMTL framework predicts that whole-organism T_{OPT} is the temperature providing maximal aerobic scope, which is governed by active-aerobic T_{CRIT}. Thus, alleviating the limits that underlie active-aerobic T_{CRIT} should allow increased maximal performance (i.e., aerobic scope) and T_{OPT} (Fig. 1). Unfortunately, few data are available comparing whole-organism T_{OPT} and aerobic scope in reptiles or amphibians. In the snake *P. regius*, whole-organism T_{OPT} and the temperature where aerobic scope is maximized appear to correspond (Fobian et al. 2014). In the toad *R. marina*, observations are more complex and suggest that the maintenance of aerobic scope to high temperatures could be independent of whole-organism T_{OPT}, at least in some cases. Hopping performance is maximized at ~30°C (Kearney et al. 2008) whereas aerobic scope can plateau at 30°C, but can also increase to at least 40°C depending on acclimation treatment (Overgaard et al. 2012). Additional data are needed to determine if acclimation elevates T_{OPT} for whole-organism performance similar to maximal aerobic scope in *R. marina*, as would be predicted by the HMTL framework.

Observations for PBT provide additional indirect evidence that whole-organism T_{OPT} corresponds to the temperature that maximizes aerobic scope in reptiles, but again data for amphibians are less clear. Generally, terrestrial ectotherms thermoregulate to within a narrow thermal range during activity if costs to thermoregulation are not prohibitively high (Huey 1982; Bauwens et al. 1995; Angilletta 2009; Kingsolver and Buckley 2015; Sears et al. 2016). Natural selection is predicted to shape thermal preference such that PBT corresponds to, or is slightly below, whole-organism T_{OPT} (Huey 1982; Bauwens et al. 1995; Angilletta et al. 2002; but see Huey and Bennett 1987). As predicted, PBT and temperature of maximum aerobic scope are highly concordant in lizards exposed to normoxic environments (Wilson 1974). On the other hand, in the boreal toad (*Anaxyrus boreas*), aerobic scope is maximal at 30°C whereas T_{PREF} is 24°C (Carey 1978, 1979). Interestingly, *A. boreas* and other anurans (*L. pipiens*, Carey 1979; *R. marina*, Overgaard et al. 2012) exhibit an increase in lactic acid production with temperatures above PBT in both resting and active animals. Increased lactic acid production indicates that high temperatures induce anaerobic respiration, even as aerobic scope is maintained, and therefore incur an oxygen debt for recovery. Further data are needed to assess whether the potential mismatch between maximal aerobic scope and T_{OPT} in anurans can be explained by animals balancing the increased costs of repaying oxygen debt resulting from increased anaerobic respiration at high temperatures with the benefits of concurrent increases in aerobic scope.

Assuming maximal aerobic scope, T_{OPT}, and PBT are linked as predicted by HMTL, they are not uniformly affected by experimental hypoxia as might initially be predicted. Only extreme hypoxia affects PBT (Fig. 2) whereas the temperature that maximizes aerobic scope and presumably whole-organism T_{OPT} is predicted to drop continuously with hypoxia (Fig. 1). This discrepancy might indicate that adult reptiles and amphibians cannot sense and respond to hypoxia-induced changes in aerobic scope in real time, which might be expected given that these animals evolved in terrestrial environments where oxygen availability is relatively stable within a lifetime. Thus, we propose that individuals choose the same body temperature regardless of the oxygen environment so long as basic metabolic demands are met, and thus predict that the "breakpoint" in Fig. 2A occurs when hypoxia causes resting-aerobic T_{CRIT} to fall below evolved PBT. Data comparing resting aerobic T_{CRIT} and PBT when oxygen environment or demand is manipulated are needed to test this prediction. Given the predicted relationships between aerobic scope, T_{OPT}, and PBT, we also expect species adapted to low-oxygen environments to have relatively lower T_{OPT} and PBT, or greater oxygen-handling capacity. However, covariation between temperature and oxygen with elevation make testing this prediction in terrestrial environments difficult.

In addition to further exploring the potential importance of resting- and active-aerobic T_{CRIT}, additional research is needed to identify the subcellular components that underlie subcellular $T_{CRIT.}$ A subset of evolutionarily conserved components might constrain thermal tolerance across a diversity of taxa, or the components that are most important could be taxonomically specific. Currently, the data needed to differentiate these possibilities are not available. We think that measures of ATPase and HSP provide useful candidates for further exploration, but caution that focusing on a single or few potential indicators in isolation will likely provide a contorted view of subcellular limitation. Advances in "-omics" technologies, particularly differential expression RNAseq, metabolomics, and proteomics could provide much useful information about subcellular physiological function, and provide additional candidate molecules for detailed analysis (e.g., Verberk et al. 2013; Williams et al. 2014; Campbell-Staton et al. 2017; Telemeco et al. 2017). We recommend that experiments manipulating the thermal and oxygen environment of organisms endeavor to collect subcellular data as well as whole-organism performance data. Where possible, an integrative approach combining measurements of subcellular components and whole-organism performance will best illuminate the mechanisms that underlie tolerance and their interactions.

Finally, the HMTL framework makes predictions for how populations could be affected by global change. Numerous species are expanding or shifting their range to higher elevations in response to climate change-related temperature increases (e.g., Sinervo et al. 2010; Pincheira-Donoso et al. 2013; Pauchard et al. 2016). However, HMTL predicts that reduced oxygen partial pressures at high elevation will lower both T_{OPT} and maximal performance. Thus, species must seek cooler environments as they move to higher elevation to maintain optimal performance, and performance potential will go down regardless of thermal environment selected. An evolutionary change appears necessary for animals to seek out reduced body temperatures because moderate hypoxia does not affect PBT (Fig. 2). The HMTL framework also predicts that species with greater oxygen capacity will be more buffered from lost performance when exposed to increased environmental temperatures. Thus, oxygen capacity might be a prime target of natural selection as climates warm, even if it does not underlie CT_{MAX} or T_{LETHAL}. Finally, given the great diversity in modes of gas exchange, metabolic demands, and shifts across life-history stages in reptiles and amphibians, we emphasize the need to explore these hypotheses in a greater number and variety of taxa.

Conclusions

Available data suggest that both subcellular- and organ-system-level mechanisms shape thermal performance and tolerance in amphibians and reptiles. The HMTL framework that we propose describes how both mechanisms co-affect animals, with their relative importance driven by their respective T_{CRIT}. We think that the HMTL hypothesis improves upon current frameworks by explicitly removing the false dichotomy between subcellular mechanisms and oxygen limitation, identifying useful parameters for further research (subcellular T_{CRIT}, resting-aerobic T_{CRIT}, and active-aerobic T_{CRIT}), and describing how aerobic and subcellular limitations interact to affect TPCs. Moreover, HMTL appears to explain a wide range of initially perplexing observations in reptiles and amphibians such as reduced aerobic scope at high temperatures without aerobic failure at critical temperatures, extreme hypoxia affecting thermal tolerance and behavior in adults with no effect of moderate hypoxia, moderate hypoxia reducing thermal tolerance in embryos, and HSP and ATPase activity suggesting loss of subcellular function near critical temperatures. Still, the HMTL framework makes numerous predictions for which additional data are needed, including animals only reducing their body temperature when resting-aerobic T_{CRIT} drops below PBT, CT_{MAX} being lower when resting-aerobic T_{CRIT} is responsible than when subcellular T_{CRIT} is responsible, maximum aerobic capacity underlying whole-organism thermal optima, and reduced performance when species invade higher elevations without increased oxygen capacity. Moreover, virtually no data are available to address the potential importance of aerobic- or subcellular-T_{CRIT} as evolutionary constraints shaping the adaptive landscape. Further data better representing the diversity of reptile and amphibian taxa are needed both to understand the potential relevance of the HMTL mechanism in extant reptiles and amphibians, and how such a mechanism could have shaped the evolution of these animals. We think that many of the ideas that make up our HMTL framework are already widely accepted within the scientific community, and hope that explicitly describing them within a single framework with clear, testable predictions will facilitate further research. Although inspired by reptiles and amphibians, this integrated framework could have broad applicability across ectothermic animals. We look forward to continued investigation further integrating, refining, and testing these ideas across mechanisms and taxa.

Acknowledgments

We are grateful to M. Angilletta, B. Bodensteiner, and J. VandenBrooks for comments on earlier drafts of this manuscript, and for the support of A. Bronikowski, T. Schwartz, B. Slater, M. Telemeco, and A. Toth.

Funding

This work was supported by Auburn University and California State University, Fresno (to R.S.T.), E.J.G. was supported by the U.S. National Science Foundation (IOS-1558071 to A. Bronikowski), the “Laboratoire d’Excellence (LABEX)” TULIP (ANR-10-LABX-41), and the European Union’s Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No 752299.

Supplementary data

Supplementary data are available at *ICB* online.

References

Al-Jassabi S. 2002. Purification and kinetic properties of skeletal muscle lactate dehydrogenase from the lizard *Agama stellio stellio*. Biochemistry (Moscow) 67:786–9.

Angilletta MJ. 2009. Thermal adaptation: a theoretical and empirical synthesis. New York (NY): Oxford University Press.

Angilletta MJ, Hill T, Robson MA. 2002. Is physiological performance optimized by thermoregulatory behavior?: A case study of the eastern fence lizard, *Sceloporus undulatus*. J Therm Biol 27:199–204.

Bartholomew GA, Tucker VA. 1963. Control of changes in body temperature, metabolism, and circulation by the Agamid lizard *Amphibolurus barbatus*. Physiol Zool 36:199–218.

Bauwens D, Garland T, Castilla AM, Van Damme R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. Evolution 49:848–63.

Bennett AF. 1973. Blood physiology and oxygen transport during activity in two lizards *Varanus gouldii* and *Sauromalus hispidus*. Comp Biochem Physiol 46:673–90.

Bennett AF, Licht P. 1972. Anaerobic metabolism during activity in lizards. J Comp Physiol 81:277–88.

Berner RA, VandenBrooks JM, Ward PD. 2007. Oxygen and evolution. Science 316:557–8.

Boyer DR. 1963. Hypoxia: effects on heart rate and respiration in the snapping turtle. Science 140:813–14.

Boyer DR. 1966. Comparative effects of hypoxia on respiratory and cardiac function in reptiles. Physiol Zool 39:307–16.

Branco LGS, Pörtner HO, Wood SC. 1993. Interaction between temperature and hypoxia in the alligator. Am J Physiol 265:R1339–43.

Brattstrom BH. 1965. Body temperatures of reptiles. Am Midl Nat 73:376–422.

Buckley LB. 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. Am Nat 171:E1–E19.

Buckley LB, Huey RB. 2016. How extreme temperatures impact organisms and the evolution of their thermal tolerance. Integr Comp Biol 56:98–109.

Burggren WW. 1988. Role of the central circulation in regulation of cutaneous gas exchange. Am Zool 28:985–98.

Cadena V, Tattersall GJ. 2009. Decreased precision contributes to the hypoxic thermoregulatory response in lizards. J Exp Biol 212:137–44.

Campbell-Staton SC, Cheviron ZA, Rochette N, Catchen J, Losos JB, Edwards SV. 2017. Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. Science 357:495–8.

Carey C. 1978. Factors affecting body temperature of toads. Oecologia 35:197–219.

Carey C. 1979. Aerobic and anaerobic energy expenditure during rest and activity in montane *Bufo b. boreas* and *Rana pipiens*. Oecologia39:213–28.

Clark TD, Sandblom E, Jutfelt F. 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. J Exp Biol 216:2771–82.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–61.

Cowles RB, Bogert CM. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull Am Mus Nat Hist 83:261–96.

Cupp PVJ. 1980. Thermal tolerance of five salientian amphibians during development and metamorphosis. Herpetologica 36:234–44.

da Silva GSF, Glass ML, Branco LGS. 2013. Temperature and respiratory function in ectothermic vertebrates. J Therm Biol 38:55–63.

Daugaard M, Rohde M, Jaattela M. 2007. The heat shock protein 70 family: highly homologous proteins with overlapping and distinct functions. FEBS Lett 581:3702–10.

Deutsch CA, Tewksbury J, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci U S A 105:6668–72.

Dillon ME, Woods HA, Wang G, Fey SB, Vasseur DA, Telemeco RS, Marshall K, Pincebourde S. 2016. Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. Integr Comp Biol 56:14–30.

DuBois PM, Shea TK, Claunch NM, Taylor EN. 2017. Effects of oxygen on responses to heating in two lizard species sampled along an elevational gradient. J Therm Biol 68:170–6.

Dupre RK, Hicks JW, Wood SC. 1986. The effect of hypoxia on evaporative cooling thresholds of lizards. J Therm Biol 11:223–7.

Eliason EJ, Clark TD, Hague MJ, Hanson LM, Gallagher ZS, Jeffries KM, Gale MK, Patterson DA, Hinch SG, Farrell AP. 2011. Differences in thermal tolerance among sockeye salmon populations. Science 332:109–12.

Ern R, Norin T, Gamperl AK, Esbaugh AJ. 2016. Oxygen dependence of upper thermal limits in fishes. J Exp Biol 219:3376–83.

Fernando P, Heikkila JJ. 2000. Functional characterization of *Xenopus* small heat shock protein, Hsp30C: the carboxyl end is required for stability and chaperone activity. Cell Stress Chaperon 5:148–59.

Fields PA. 2001. Review: protein function at thermal extremes: balancing stability and flexibility. Comp Biochem Physiol A 129:417–31.

Flewelling S, Parker SL. 2015. Effects of temperature and oxygen on growth and differentiation of embryos of the ground skink, *Scincella lateralis*. J Exp Zool 323:445–55.

Floyd RB. 1983. Ontogenetic change in the temperature tolerance of larval *Bufo marinus* (Anura: bufonidae). Comp Biochem Physiol 75:267–71.

Fobian D, Overgaard J, Wang T. 2014. Oxygen transport is not compromised at high temperature in pythons. J Exp Biol 217:3958–61.

Frederich M, Pörtner HO. 2000. Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. Am J Physiol 279:R1531–8.

Gangloff EJ, Holden KG, Telemeco RS, Baumgard LH, Bronikowski AM. 2016. Hormonal and metabolic responses to upper temperature extremes in divergent life-history ecotypes of a garter snake. J Exp Biol 219:2944–54.

Gao J, Zhang W, Dang W, Mou Y, Gao Y, Sun BJ, Du WG. 2014. Heat shock protein expression enhances heat tolerance of reptile embryos. Proc Biol Sci 281:20141135.

Giomi F, Fusi M, Barausse A, Mostert B, Pörtner HO, Cannicci S. 2014. Improved heat tolerance in air drives the recurrent evolution of air-breathing. Proc Biol Sci 281:20132927.

Glass ML, Johansen K, Abe AS. 1981. Pulmonary diffusing capacity in reptiles (relations to temperature and O_2-uptake). J Comp Physiol 142:509–14.

Gleeson TT. 1991. Patterns of metabolic recovery from exercise in amphibians and reptiles. J Exp Biol 160:187–207.

Gräns A, Jutfelt F, Sandblom E, Jönsson E, Wiklander K, Seth H, Olsson C, Dupont S, Ortega-Martinez O, Einarsdottir I, et al. 2014. Aerobic scope fails to explain the detrimental effects on growth resulting from warming and elevated CO_2 in Atlantic halibut. J Exp Biol 217:711–17.

Gunderson AR, Stillman JH. 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proc R Soc B 282:20150401.

Heatwole H, Firth B, Webb G. 1973. Panting thresholds of lizards-I. Some methodological and internal influences on the panting threshold of an agamid, *Amphibolurus muricatus*. Comp Biochem Physiol A 46:799–826.

Helmuth B, Kingsolver JG, Carrington E. 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? Annu Rev Physiol 67:177–201.

Hicks JW, Wang T. 2004. Hypometabolism in reptiles: behavioural and physiological mechanisms that reduce aerobic demands. Resp Physiol Neurobiol 141:261–71.

Hicks JW, Wood SC. 1985. Temperature regulation in lizards: effects of hypoxia. Am Physiol 248:R595–600.

Hochachka PW, Somero GN. 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford (UK): Oxford University Press.

Huey RB. 1982. Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH, editors. Biology of the reptilia. New York (NY): Academic Press. p. 25–74.

Huey RB, Bennett AF. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. Evolution 41:1098–115.

Huey RB, Berrigan D. 2001. Temperature, demography, and ectotherm fitness. Am Nat 158:204–10.

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: roles of behavior, physiology and adaptation. Philos Trans R Soc B 367:1665–79.

Huey RB, Losos JB, Moritz C. 2010. Are lizards toast? Science 328:832–3.

Huey RB, Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: discussion of approaches. Am Zool 19:357–66.

Hutchison VH, Whitford WG, Kohl M. 1968. Relation of body size and surface area to gas exchange in anurans. Physiol Zool 41:65–85.

Irie M, Nitta K, Nonaka T. 1998. Biochemistry of frog ribonucleases. Cell Mol Life Sci 54:775–84.

Jackson DC. 2007. Temperature and hypoxia in ectothermic tetrapods. J Therm Biol 32:125–33.

Jutfelt F, Gräns A, Jönsson E, Wiklander K, Seth H, Olsson C, Dupont S, Ortega-Martinez O, Sundell K, Axelsson M. 2014. Response to 'How and how not to investigate the oxygen and capacity limitation of thermal tolerance (OCLTT) and aerobic scope - remarks on the article by Gräns et al.'. J Exp Biol 217:4433–5.

Jutfelt F, Norin T, Ern R, Overgaard J, Wang T, McKenzie DJ, Lefevre S, Nilsson GE, Metcalfe NB, Hickey AJR, et al. 2018. Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology. J Exp Biol 221: jeb169615.

Kearney M. 2012. Metabolic theory, life history and the distribution of a terrestrial ectotherm. Funct Ecol 26:167–79.

Kearney M. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. Ecol Lett 16:1470–9.

Kearney M, Phillips BL, Tracy CR, Christian KA, Betts G, Porter WP. 2008. Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. Ecography 31:423–34.

Kearney M, Porter WP. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol Lett 12:334–50.

Kingsolver JG, Buckley LB. 2015. Climate variability slows evolutionary responses of *Colias* butterflies to recent climate change. Proc Biol Sci 282:20142470.

Kingsolver JG, Woods HA. 2016. Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. Am Nat 187:283–94.

Kinney JL, Matsuura DT, White FN. 1977. Cardiorespiratory effects of temperature in the turtle, *Pseudemys floridana*. Resp Physiol 31:309–25.

Klok CJ, Sinclair BJ, Chown SL. 2004. Upper thermal tolerance and oxygen limitation in terrestrial arthropods. J Exp Biol 207:2361–70.

Kregel K. 2002. Heat shock proteins: modifying factors in physiological stress response and acquired thermotolerance. J Appl Physiol 92:2177–86.

Kuramoto M. 1975. Adaptive significance in oxygen consumption of frog embryos in relation to the environmental temperatures. Comp Biochem Physiol 52:59–62.

Levy O, Buckley LB, Keitt TH, Smith CD, Boateng KO, Kumar DS, Angilletta MJ. 2015. Resolving the life cycle alters expected impacts of climate change. Proc Biol Sci 282:20150837.

Liang L, Sun BJ, Ma L, Du WG. 2015. Oxygen-dependent heat tolerance and developmental plasticity in turtle embryos. J Comp Physiol B 185:257–63.

Licht P. 1964. The temperature dependence of myosin-adenosinetriphosphatase and alkaline phosphatase in lizards. Comp Biochem Physiol 12:331–40.

Lucassen M, Koschnick N, Eckerle LG, Pörtner HO. 2006. Mitochondrial mechanisms of cold adaptation in cod (*Gadus morhua* L.) populations from different climatic zones. J Exp Biol 209:2462–71.

Malishev M, Bull CM, Kearney MR. 2018. An individual-based model of ectotherm movement integrating metabolic and microclimatic constraints. Methods Ecol Evol 9:472–89.

McCue MD, De Los Santos R. 2013. Upper thermal limits of insects are not the result of insufficient oxygen delivery. Physiol Biochem Zool 86:257–65.

McMillan DM, Irschick DJ, Rees BB. 2011. Geographic variation in the effects of heat exposure on maximum sprint speed and Hsp70 expression in the western fence lizard *Sceloporus occidentalis*. Physiol Biochem Zool 84:573–82.

Norin T, Malte H, Clark TD. 2014. Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. J Exp Biol 217:244–51.

Overgaard J, Andersen JL, Findsen A, Pedersen PB, Hansen K, Ozolina K, Wang T. 2012. Aerobic scope and cardiovascular oxygen transport is not compromised at high temperatures in the toad *Rhinella marina*. J Exp Biol 215:3519–26.

Pauchard A, Milbau A, Albihn A, Alexander J, Burgess T, Daehler C, Englund G, Essl F, Evengård B, Greenwood GB, et al. 2016. Non-native and native organisms moving into high elevation and high latitude ecosystems in an era of climate change: new challenges for ecology and conservation. Biol Invasion 18:345–53.

Paulson BK, Hutchison VH. 1987. Blood changes in *Bufo cognatus* following acute heat stress. Comp Biochem Physiol 87:461–6.

Pincheira-Donoso D, Tregenza T, Witt MJ, Hodgson DJ. 2013. The evolution of viviparity opens opportunities for lizard radiation but drives it into a climate cul-de-sac. Global Ecol Biogeogr 2013:1–11.

Pinder AW, Friet SC. 1994. Oxygen transport in egg masses of the amphibians *Rana sylvatica* and *Ambystoma maculatum*: convection, diffusion, and oxygen production by algae. J Exp Biol 197:17–30.

Pörtner HO. 2014. How and how not to investigate the oxygen and capacity limitation of thermal tolerance (OCLTT) and aerobic scope - remarks on the article by Gräns et al. J Exp Biol 217:4432–3.

Pörtner HO. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. Naturwissenschaften 88:137–46.

Pörtner HO. 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp Biochem Physiol A 132:739–61.

Pörtner HO, Bock C, Mark FC. 2017. Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. J Exp Biol 220:2685–96.

Pörtner HO, Gutt J. 2016. Impacts of climate variability and change on (marine) animals: physiological underpinnings and evolutionary consequences. Integr Comp Biol 56:31–44.

Pörtner HO, Knust R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315:95–7.

Pörtner HO, MacLatchy LM, Toews DP. 1991. Metabolic responses of the toad *Bufo marinus* to environmental hypoxia: an analysis of the critical P_{O2}. Physiol Zool 64:836–49.

Pough FH. 1980. Blood oxygen transport and delivery in reptiles. Am Zool 20:173–85.

Rezende EL, Castañeda LE, Santos M, Fox C. 2014. Tolerance landscapes in thermal ecology. Funct Ecol 28:799–809.

Rohr JR, Raffel TR. 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. Proc Natl Acad Sci U S A 107:8269–74.

Rollinson N, Rowe L. 2018. Oxygen limitation at the larval stage and the evolution of maternal investment per offspring in aquatic environments. Am Nat 191 published online (doi:10.1086/696857).

Sacerdote AB, King RB. 2009. Dissolved oxygen requirements for hatching success of two ambystomatid salamanders in restored ephemeral ponds. Wetlands 29:1202–13.

Schulte PM. 2015. The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. J Exp Biol 218:1856–66.

Sears MW, Angilletta MJJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA. 2016. Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. Proc Natl Acad Sci U S A 113:10595–600.

Seebacher F, Franklin CE. 2011. Physiology of invasion: cane toads are constrained by thermal effects on physiological mechanisms that support locomotor performance. J Exp Biol 214:1437–44.

Seebacher F, White CR, Franklin CE. 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. Nat Clim Change 5:61–6.

Seymour RS, Bradford DF. 1995. Respiration of amphibian eggs. Physiol Zool 68:1–25.

Shea TK, DuBois PM, Claunch NM, Murphey NE, Rucker KA, Brewster RA, Taylor EN. 2016. Oxygen concentration affects upper thermal tolerance in a terrestrial vertebrate. Comp Biochem Physiol A 199:87–94.

Sheldon KS, Dillon ME. 2016. Beyond the mean: biological impacts of cryptic temperature change. Integr Comp Biol 56:110–19.

Sherman E. 1980. Ontogenetic change in thermal tolerance of the toad *Bufo woodhousii fowleri*. Comp Biochem Physiol 65:227–30.

Simoniello P, Esposito MG, Trinchella F, Motta CM, Scudiero R. 2016. Alterations in brain morphology and HSP70 expression in lizard embryos exposed to thermal stress. C R Biol 339:380–90.

Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Cruz MV-S, Lara-Resendiz R, Martinez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–9.

Smith C, Telemeco RS, Angilletta MJ, VandenBrooks JM. 2015. Oxygen supply limits the heat tolerance of lizard embryos. Biol Lett 11:20150113.

Snyder GK, Weathers WW. 1975. Temperature adaptations in amphibians. Am Nat 109:93–101.

Spotila JR. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol Monogr 42:95–125.

Steiner AA, Branco LG. 2002. Hypoxia-induced anapyrexia: implications and putative mediators. Annu Rev Physiol 64:263–88.

Storch D, Menzel L, Frickenhaus S, Pörtner HO. 2014. Climate sensitivity across marine domains of life: limits to evolutionary adaptation shape species interactions. Global Change Biol 20:3059–67.

Sunday JM, Bates AE, Dulvy NK. 2011. Global analysis of thermal tolerance and latitude in ectotherms. Proc Biol Sci 278:1823–30.

Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc Natl Acad Sci U S A 111:5610–15.

Tattersall GJ, Cadena V, Skinner MC. 2006. Respiratory cooling and thermoregulatory coupling in reptiles. Respir Physiol Neurobiol 154:302–18.

Tattersall GJ, Gerlach RM. 2005. Hypoxia progressively lowers thermal gaping thresholds in bearded dragons, *Pogona vitticeps*. J Exp Biol 208:3321–30.

Teague C, Youngblood JP, Ragan K, Angilletta MJ, Jr, VandenBrooks JM. 2017. A positive genetic correlation between hypoxia tolerance and heat tolerance supports a controversial theory of heat stress. Biol Lett 13:20170309.

Tedeschi JN, Kennington WJ, Tomkins JL, Berry O, Whiting S, Meekan MG, Mitchell NJ. 2016. Heritable variation in heat shock gene expression: a potential mechanism for adaptation to thermal stress in embryos of sea turtles. Proc R Soc B 283:20152320.

Telemeco RS. 2014. Immobile and mobile life-history stages have different thermal physiologies in a lizard. Physiol Biochem Zool 87:203–15.

Telemeco RS, Gangloff EJ, Cordero GA, Polich RL, Bronikowski AM, Janzen FJ. 2017. Physiology at near-critical temperatures, but not critical limits, varies between two lizard species that partition the thermal environment. J Anim Ecol 86:1510–22.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, De Siqueira MF, Grainger A, Hannah L, et al. 2004. Extinction risk from climate change. Nature 427:145–8.

Ulmasov KA, Shammakov S, Karaev K, Evgen'ev MB. 1992. Heat shock proteins and thermoresistance in lizards. Proc Natl Acad Sci U S A 89:1666–70.

Ultsch GR. 1973. A theoretical and experimental investigation of the relationship between metabolic rate, body size, and oxygen exchange capacity. Respir Physiol 18:143–60.

Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CD, McCann KS, Savage V, Tunney TD, O'Connor MI. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proc Biol Sci 281:20132612.

Verberk WCEP, Leuven RSEW, van der Velde G, Gabel F, Overgaard J. 2018. Thermal limits in native and alien freshwater peracarid Crustacea: the role of habitat use and oxygen limitation. Funct Ecol published online (doi:10.1111/1365-2435.13050).

Verberk WCEP, Overgaard J, Ern R, Bayley M, Wang T, Boardman L, Terblanche JS. 2016. Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. Comp Biochem Physiol A 192:64–78.

Verberk WCEP, Sommer U, Davidson RL, Viant MR. 2013. Anaerobic metabolism at thermal extremes: a metabolomic test of the oxygen limitation hypothesis in an aquatic insect. Integr Comp Biol 53:609–19.

Vitt LJ, Caldwell JP. 2009. Herpetology: an introductory biology of amphibians and reptiles. New York (NY): Academic Press.

Wang T. 2011. Gas exchange in frogs and turtles: how ectothermic vertebrates contributed to solving the controversy of pulmonary oxygen secretion. Acta Physiol 202:593–600.

Wang T, Branco LGS, Glass ML. 1994. Ventilatory responses to hypoxia in the toad *Bufo paracnemis* before and after a decrease in haemoglobin oxygen-carrying capacity. J Exp Biol 186:1–8.

Wang T, Hicks JW. 2004. Why savannah monitor lizards hyperventilate during activity: a comparison of model predictions and experimental data. Respir Physiol Neurobiol 144:251–61.

Wang T, Lefevre S, Iversen NK, Findorf I, Buchanan R, McKenzie DJ. 2014. Anaemia only causes a small reduction in the upper critical temperature of sea bass: is oxygen delivery the limiting factor for tolerance of acute warming in fishes? J Exp Biol 217:4275–8.

Whitford WG. 1973. The effects of temperature on respiration in the amphibia. Am Zool 13:505–12.

Whitford WG, Hutchison VH. 1965. Gas exchange in salamanders. Physiol Zool 38:228–42.

Williams CM, Buckley LB, Sheldon KS, Vickers M, Portner HO, Dowd WW, Gunderson AR, Marshall KE, Stillman JH. 2016. Biological impacts of thermal extremes: mechanisms and costs of functional responses matter. Integr Comp Biol 56:73–84.

Williams CM, Watanabe M, Guarracino MR, Ferraro MB, Edison AS, Morgan TJ, Boroujerdi AF, Hahn DA. 2014. Cold adaptation shapes the robustness of metabolic networks in *Drosophila melanogaster*. Evolution 68:3505–23.

Wilson KJ. 1974. The relationship of oxygen supply for activity to body temperature in four species of lizards. Copeia 1974:920–34.

Winwood-Smith HS, Alton LA, Franklin CE, White CR. 2015. Does greater thermal plasticity facilitate range expansion of an invasive terrestrial anuran into higher latitudes? Conserv Phys 3. doi: 10.1093/conphys/cov010.

Withers PC, Hillman SS. 1983. The effects of hypoxia on pulmonary function and maximal rates of oxygen consumption in two anuran amphibians. J Comp Physiol B 152:125–9.

Wood SC. 1990. Effect of hematocrit on behavioral thermoregulation of the toad *Bufo marinus*. Am J Physiol 258:R848–51.

Wood SC, Gonzales R. 1996. Hypothermia in hypoxic animals: mechanisms, mediators, and functional significance. Comp Biochem Physiol 113:37–43.

Wood SC, Moberly WR. 1970. The influence of temperature on the respiratory properties of iguana blood. Respir Physiol 10:20–9.

Woods HA. 1999. Egg-mass size and cell size: effects of temperature on oxygen distribution. Am Zool 39:244–52.

Zatsepina OG, Ulmasov KA, Beresten SF, Molodtsov VB, Rybtsov SA, Evgen'ev MB. 2000. Thermotolerant desert lizards characteristically differ in terms of heat-schock system regulation. J Exp Biol 203:1017–25.

Integrative and Comparative Biology
Integrative and Comparative Biology, volume 58, number 1, pp. 25–37
doi:10.1093/icb/icy012
Society for Integrative and Comparative Biology

INVITED PERSPECTIVES

Intraspecific Variation in the Information Content of an Ornament: Why Relative Dewlap Size Signals Bite Force in Some, But Not All Island Populations of *Anolis sagrei*

Simon Baeckens,[1,*,†] Tess Driessens,[*] Katleen Huyghe,[*] Bieke Vanhooydonck[*] and Raoul Van Damme[*]

*Laboratory of Functional Morphology, Department of Biology, University of Antwerp, Universiteitsplein 1, Wilrijk 2610, Belgium; †Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

The first two authors contributed equally to this work.

[1] E-mail: simon.baeckens@uantwerp.be

Synopsis In many animals, male secondary sexual traits advertise reliable information on fighting capacity in a male–male context. The iconic sexual signaling device of anole lizards, the dewlap, has been extensively studied in this respect. For several territorial anole species (experiencing strong intrasexual selection), there is evidence for a positive association between dewlap size and bite capacity, which is an important determinant of combat outcome in lizards. Intriguingly, earlier studies did not find this expected correlation (relative dewlap size–relative bite force) in the highly territorial brown anole lizard, *Anolis sagrei*. We hypothesize that the dewlap size–bite force relationship can differ among populations of the same species due to interpopulation variation in the degree of male–male competition. In line with this thought, we expect dewlap size to serve as a reliable predictor of bite performance only in those populations where the level of intrasexual selection is high. To tackle this hypothesis, we examined the relationship between male dewlap size and bite force on the intraspecific level in *A. sagrei*, using an extensive dataset encompassing information from 17 island populations distributed throughout the Caribbean. First, we assessed and compared the relationship between both variables in the 17 populations under study. Second, we linked the relative dewlap size–bite force relationship within each population to variation in the degree of intrasexual selection among populations, using sexual size dimorphism and dewlap display intensity as surrogate measures. Our results showed that absolute dewlap size is an excellent predictor of maximum bite force in nearly all *A. sagrei* populations. However, relative dewlap size is only an honest signal of bite performance in 4 out of the 17 populations. Surprisingly, the level of signal honesty did not correlate with the strength of intrasexual selection. We offer a number of conceptual and methodological explanations for this unexpected finding.

Introduction

The evolution of male secondary sexual traits, such as the colossal antlers in deer or the giant horns in rhinoceros beetles, has fascinated biologists ever since Darwin (1871; Andersson 1982; Bradbury and Vehrencamp 1998; Emlen 2008). These elaborate sexual traits can function as real weapons to overpower or even kill male opponents (e.g., mandibles of male fig wasps; Bean and Cook 2001), but also as reliable signals advertising "fighting capacity" without playing a role during actual physical combats (e.g., red coloration in male mandrills; Setchell and Wickings 2005). Traits that honestly signal fighting capacity seem highly beneficial to predict contest outcomes and thereby avoid the costly interactions physical combats may impose (Andersson 1994). This is especially true for species where actual fights between males can result in serious body damage and even in death (e.g., wasps, Bean and Cook 2001; Abe et al. 2003; spiders, Leimar et al. 1991). The idea that male secondary sexual signals communicate reliable information about quality in an intrasexual context has been evidenced by a variety of studies showing a direct link between variation in signal design

Advance Access publication May 31, 2018

(especially size and color) and the ability to win male contests (e.g., Jennions and Backwell 1996; Panhuis and Wilkinson 1999; Alonso-Alvarez et al. 2004). In many cases, the size of these sexual traits correlates strongly with overall body size (arguably the most important predictor of contest outcome (e.g., Clutton-Brock et al. 1979; Hughes 1996; Karsten et al. 2009; Hardy and Briffa 2013), and as such acts as a redundant or back-up signal (Zuk et al. 1992; Johnstone 1996; Candolin 2003) when advertising fighting capacity. However, in at least some cases, the size of secondary sexual traits reveals more than just the carrier's overall body size during agonistic interactions. Here, sexual signal size contains information on fighting capacity independent of overall body size (i.e., relative size), and can therefore be considered as a reliable signal in itself. In dung beetles, for example, relative male horn size accurately predicts pulling force and maximal exertion, two ecologically relevant performance measures associated with fighting success in beetles (Lailvaux et al. 2005). Also in lizards, male signals can act as size-free indices of fighting capacity, quantified by endurance or bite force (e.g., Perry et al. 2004; Lappin and Husak 2005; Vanhooydonck et al. 2005a). Anole lizards in particular have received considerable attention in this respect (e.g., Lailvaux et al. 2004; Vanhooydonck et al. 2005b; Lailvaux and Irschick 2007). They typically have an extendible throat fan, called a dewlap. This sexually selected trait is generally far more elaborated in the male sex and is exceptional for its high degree of interspecific variation in design (Nicholson et al. 2007; Johnson and Wade 2010). Besides, anoles exhibit varying degrees of territoriality and male–male competition (Losos 2009; Johnson et al. 2009; Kamath and Losos 2017), also reflected by their remarkable diversity in sexual size dimorphism (SSD; i.e., predominantly male-biased SSD) (Stamps et al. 1997; Ord et al. 2001; Butler et al. 2007).

One obvious question that arises is whether dewlap size indicates fighting capacity in *Anolis* lizards? The evidence is rather mixed. In highly territorial, sexually dimorphic (high-SSD) species (i.e., *A. carolinensis*, *A. cristatellus*, *A. evermanni*, *A. gundlachi*, and *A. lineatopus*), relative dewlap size predicts bite force and thus seems to contain detailed information on fighting capacity (Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007). However, no such relationship was found in less dimorphic (low-SSD) species (i.e., *A. angusticeps*, *A. distichus*, and *A. valencienni*; Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007). The authors explain the lack of this relation in less dimorphic species preliminary by a low degree of territoriality. Bite performance, in particular, might be far less important for males of species that do not actively defend territories or that do not experience a high degree of male–male competition associated with vigorous fights. Lailvaux and Irschick (2007) further corroborated this idea by showing that bite force predicted male combat success only in the high-SSD species and that the incidence of biting increased with SSD.

Intriguingly, one species in their dataset defied this putative principle: *Anolis sagrei*, albeit clearly sexually dimorphic, did not show the expected positive correlation between relative dewlap size and bite performance (although a significant relationship was found between absolute dewlap size and bite force). In accordance, Driessens et al. (2015) also failed to find such a relationship in wild-caught males from Florida, when looking at relative indices. Because of these unexpected results, we aimed to further explore the dewlap size–bite force relationship in this polygynous and highly territorial species (Schoener and Schoener 1980; Tokarz 1998, 2002). Direct physical combats are commonly observed among brown anole males and primarily involve biting, jaw sparring, and interlocking (Scott 1984; Tokarz 1985, 1987; McMann 2000; Steffen and Guyer 2014; Driessens et al. 2014). *Anolis sagrei* has a yellow-to-reddish dewlap that can show dramatic intraspecific variation in size, color, pattern, and even use (Vanhooydonck et al. 2009; Edwards and Lailvaux 2012; Driessens et al. 2017). Adult males primarily use dewlap displays in combination with push-ups and head-bobs for territorial defense and/or for access to females (e.g., Scott 1984; Simon 2011; Driessens et al. 2014). Recently, display behavior and dewlap color have been reported to predict the outcome of staged contests between size-matched males (Steffen and Guyer 2014), further demonstrating the role of the *A. sagrei* dewlap in signaling quality to opponents (but see Tokarz et al. 2003). Close-proximity contest experiments additionally revealed that *A. sagrei* males with enhanced biting capacities are at a competitive advantage for winning fights (Lailvaux and Irschick 2007), highlighting the importance of signaling bite capacity too, during agonistic interactions.

The main goal of this study is to look in more detail at the relationship between male dewlap size and bite force, explicitly for *A. sagrei*. Therefore, we took an intraspecific comparative approach, documenting and comparing this specific relationship in 17 *A. sagrei* island populations distributed across the Caribbean. We looked at the relationship between dewlap size and bite force, using absolute as well as relative indices. Consistent with previous studies, we expected absolute dewlap size to be a good predictor of absolute bite force for each study population (Lailvaux and Irschick 2007; Cox et al. 2009; Driessens et al. 2015). However, we hypothesize that the relative dewlap size–bite force relationship will differ among populations due to interpopulation variation in the degree of male–male competition. In line with this thought, we expect dewlap size to serve as a reliable predictor of bite performance only in those populations where the level of intrasexual selection is high (following Lailvaux and Irschick 2007). To do so, we linked the dewlap size–bite force relationship within each population to both SSD and display intensity (DI) among populations, taking into account phylogenetic relationships.

Materials and methods

Animals

We sampled a total of 639 adult *A. sagrei* males from 17 populations distributed across the Caribbean (Fig. 1). Sampling localities included Acklins, Andros, Chub Cay, Crooked Island, Grand Bahama, Pidgeon Cay, Staniel Cay (data collection for these seven populations occurred in April–May 2003), Jamaica (March 2012), Cuba (Santa Clara, Soroa 1, Soroa 2; April–May 2012), San Salvador (January 2013), Cayman Islands (Cayman Brac, Grand Cayman, Little Cayman; March 2013), South Abaco, and South Bimini (March 2015). Since previous studies on *A. carolinensis* have reported a significant effect of seasonality on dewlap size, bite force, and display behavior (Jenssen et al. 1995, 2001; Irschick et al. 2006; Lailvaux et al. 2015), data were collected during the *A. sagrei* breeding season (March–September, Lee et al. 1989), apart from one population (i.e., San Salvador) that was sampled in January. We caught 404 *A. sagrei* males by noose and kept them individually in plastic bags for maximum 48 h, before releasing them back at the location of capture. For these individuals, we measured morphology, quantified dewlap size, and carried out standard bite force measurements. Another 235 male individuals (but only for ten populations) were video-recorded while behaving in their natural habitat.

Morphology

We measured the lizards' snout–vent length (SVL) and head length (HL; from the tip of the snout to the posterior edge of the parietal scale) using digital calipers (Mitutoyo CD-15DC, accuracy 0.01 mm). For measuring dewlap size, lizards were first positioned on their left side against a 1-cm^2 gridded paper. We then gently pulled the base of the ceratobranchial forward with a pair of forceps until the dewlap was fully extended parallel to the grid (Bels 1990). Next, we photographed the dewlap, using a Nikon D70 camera mounted on a tripod. Last, Adobe Photoshop CS3 extended software (AP CS3, version 10.0) was used to trace the outer edge of the dewlap on the digital images and to calculate absolute dewlap area. This standard method for measuring dewlap dimensions has produced highly repeatable results in a previous study (Vanhooydonck et al. 2005a).

Bite force

Standard methods were used to measure maximum bite force. Briefly, we encouraged lizards to bite on two metal plates connected to an isometric Kistler force transducer (type 9203) and charge amplifier (type 5995); for detailed descriptions of setup and biting procedure, see Herrel et al. (1999a) and Vanhooydonck et al. (2005b). Each individual was subjected to a total of five bite trials with approximately 30 min in between (as in e.g., Herrel et al. 2001; Lailvaux et al. 2004; Irschick et al. 2006; Lailvaux and Irschick 2007). The highest of the five bite force measurements was then used as the maximal bite force capacity in each individual. The applied methodology has been widely used and shown to be effective for obtaining maximal bite forces in lizards (e.g., Herrel et al. 2001; Lailvaux et al. 2004; Vanhooydonck et al. 2005b; Lailvaux and Irschick 2007; Baeckens et al. 2017). Since temperature is known to affect bite performance (Bennett 1985; Herrel et al. 1999b; Anderson et al. 2008), we made sure every lizard had a body temperature between 29°C and 31°C prior to every bite trial (the average field-active body temperature of *A. sagrei* is 30.6°C; Losos 2009). Body temperature was verified using a cloacal thermometer (APPA51, K-type).

Sexual size dimorphism

Consistent with Lailvaux and Irschick (2007, and references therein), we calculated SSD as mean SVL in males divided by mean SVL in females. Values of SSD were calculated for each population, and only SVLs of mature males and females were included.

Display intensity

As in Driessens et al. (2017), we recorded the natural behavior of 20–30 males per population (ten study populations) for a timespan of 10 min, using a high-definition camera (Sony, HDR-CX260VE). First, we located lizards by walking slowly through their natural habitat until an apparently undisturbed individual was spotted. Next, we started filming the lizard's

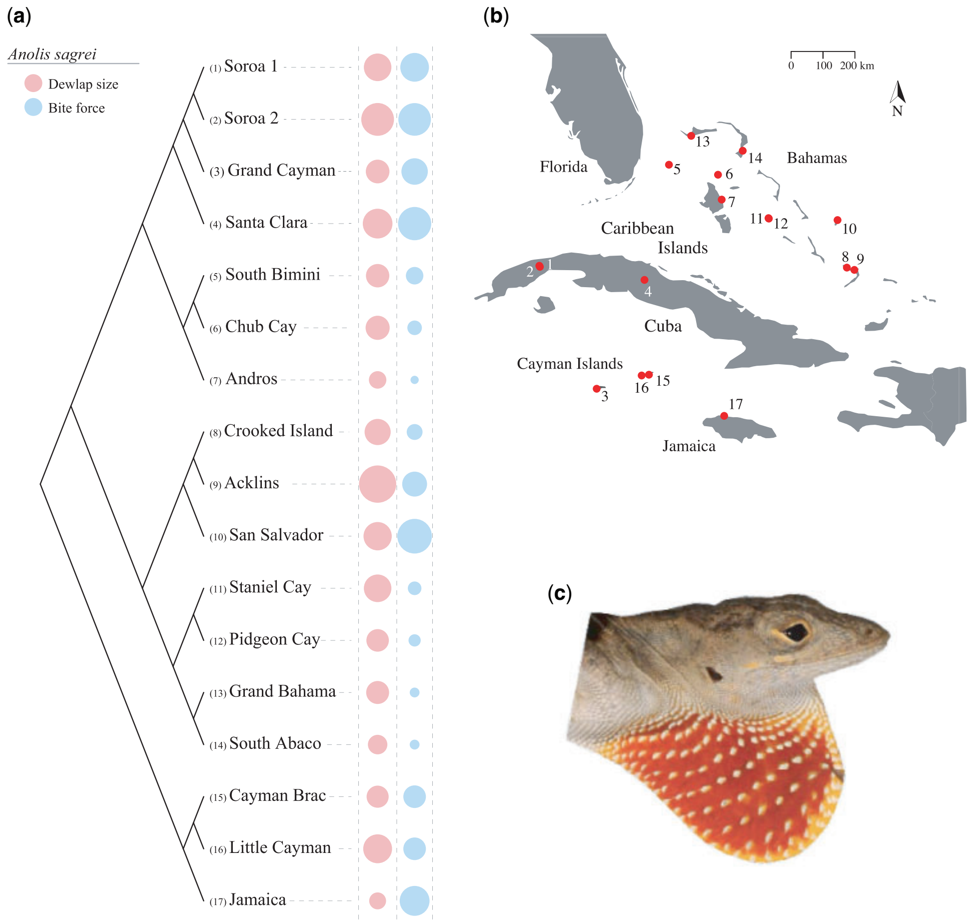


Fig. 1 (**a**) Phylogenetic relationships among the 17 *Anolis sagrei* study populations presented with corresponding sampling sites (**b**) distributed across the Caribbean. Circle size represents the mean dewlap size (*red*) and bite force (*blue*) of a population. Photograph (**c**) showing the large dewlap of a male *A. sagrei* lizard.

behavior from approximately 5–15 m using the camera zoom function (30× optical zoom), in order to minimize disturbances caused by our presence. Video recordings were only made during sunny or partly cloudy conditions to avoid possible confounding effects of weather on the lizard's activity level (Huey 1982; Hertz et al. 1993). All behavioral recordings were scored offline, using JWatcher event-recorder software (Blumstein and Daniel 2007). For each focal individual, we noted the number and duration of three main display types: head-nods (up-and-down movement of the head), push-ups (up-and-down movement of the body and tail caused by flexion of the legs), and dewlap extensions (pulsing of the dewlap). These displays can function in species recognition (e.g., Rand and Williams 1970; Losos 1985), in predator deterrence (e.g., Leal and Rodríguez-Robles 1995, 1997), but most often in social and sexual communication (e.g., Greenberg and Noble 1944; Jenssen 1970; Crews 1975; Carpenter 1978; Driessens et al. 2014; Baeckens et al. 2016). Moreover, DI is typically inter-correlated in the sense that males that frequently perform one display type also exhibit the other types at a high rate (e.g., Scott 1984; McMann 2000; Driessens et al. 2014; Steffen and Guyer 2014). In the remaining, "DI" refers to the proportion of time that individuals spent displaying in their natural setting during the 10 min observation period (averaged per population).

Statistical analyses

Prior to statistical analyses, data on HL, dewlap size, bite force, and SSD were $\log_{10}$-transformed. Proportion data (i.e., DI) were normalized via arcsin-square root transformation (Sokal and Rohlf 1995). In all cases, assumptions of normality were confirmed using Shapiro–Wilk tests, and probabilities (P) lower than 0.05 were considered significant.

All statistical tests involving dewlap size and bite force were done with absolute as well as relative (i.e., size-corrected) data. Consistent with Vanhooydonck et al. (2005a) and Lailvaux and Irschick (2007), we used HL for removing effects of overall size. This metric strongly correlated with dewlap size and bite force, and has previously proven to be most appropriate for calculating relative indices of these two variables (Vanhooydonck et al. 2005a; Herrel and O'Reilly 2006). Relative bite force and dewlap size were calculated by regressing $\log_{10}$ bite force and $\log_{10}$ dewlap size against $\log_{10}$ HL and, subsequently, by extracting the residual values for all individuals.

We first ran a univariate general linear model (GLM) to test whether the relationship between dewlap size and bite force (independent and dependent variable, respectively) differed among our study populations. HL was then added to the model as a covariate, to assess the same effects after size correction. Both GLM analyses revealed significant dewlap size * population interaction effects on bite force, which impelled us to subsequently examine this relationship separately within populations. We therefore carried out linear regressions per population with dewlap size as independent and bite force as dependent variable. Following Lailvaux and Irschick (2007), we obtained relative indices by regressing dewlap size and bite force against HL and calculating the residuals for all individuals per population. We then ran a second set of linear regressions, this time with relative bite force against relative dewlap size (i.e., residuals; consistent with Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007).

Among-population analyses were performed in an explicit phylogenetic context in order to account for the non-independency of our data points (Felsenstein 1985; Harvey and Pagel 1991). We used the phylogenetic tree proposed by Driessens et al. (2017) in all phylogenetic comparative analyses. Driessens' tree was created using the exact same populations sampled in this study. To test the idea that reliable information content of the dewlap in itself depends on the local intensity of intrasexual selection, we regressed the slope of the relative "dewlap size–bite force" regression line for each population (i.e., coefficient *b*) against SSD and DI, respectively. We here employed phylogenetic generalized least squares (pgls) regressions with incorporation of phylogenetic relationships on population level (caper package R, Orme et al. [2013]; for a detailed description of the used phylogenetic tree, see Driessens et al. 2017). This method uses maximum likelihood to simultaneously estimate the regression model and phylogenetic signal (Pagel's λ) of the residual error (Garland and Ives 2000; Revell 2010), and has shown to do better than a priori tests of phylogenetic signal; especially when sample sizes are smaller than 20 (Blomberg et al. 2003; Revell 2010; Kamilar and Cooper 2013). Because data from one population (i.e., San Salvador) could only be collected outside the breeding season, we ran an additional set of the same pgls regression analyses excluding these particular data.

Results

Population means and standard deviations for tested variables are provided in Table 1. The relationship between dewlap size and bite force differed significantly among populations ($F_{16,\ 381} = 14.93$, $P < 0.0001$), also after correcting for body size ($F_{16,\ 380} = 9.36$, $P < 0.0001$). Within-population regression analyses revealed that absolute dewlap size is an excellent predictor of absolute bite force in nearly all study populations ($R > 0.65$, $P < 0.005$, Table 2); only for the population of Santa Clara the relationship failed to reach the conventional level of statistical significance ($R = 0.38$, $P = 0.054$). However, after correcting for body size, in only 4 out of the 17 tested populations, relative dewlap size still exhibited a significant positive relationship with bite force (Table 2 and Fig. 2). We additionally observed that these results based on relative indices varied widely across populations with estimated slopes ranging from −0.353 in Little Cayman to +0.729 in South Abaco (Table 2). Overall, results of the population sampled outside the breeding season (i.e., San Salvador) did not deviate from the other study populations sampled during the reproductive cycle in *A. sagrei* (both absolute and relative indices, Tables 1 and 2 and Fig. 1).

An among-population regression analysis (pgls) failed to find a significant association between the relative dewlap size–bite force relationship (i.e., slope coefficient *b*) and SSD ($R = 0.11$, $\mathrm{df} = 16$, $P = 0.662$). Thus, in populations characterized by larger SSD, dewlap size in itself was not a more reliable signal of bite force than in populations characterized by lower SSD. The same applies to DI, as no significant correlation was found between the relative dewlap size–bite force relationship and DI ($R = 0.23$, $\mathrm{df} = 9$, $P = 0.532$). Excluding the population of San Salvador from the pgls regressions did not alter any of our results (results remained non-significant, SSD: $R = 0.12$, $\mathrm{df} = 15$, $P = 0.657$ and DI: $R = 0.13$, $\mathrm{df} = 8$, $P = 0.747$).

Discussion

By studying a series of island populations, we here present our findings on the reliability of dewlap

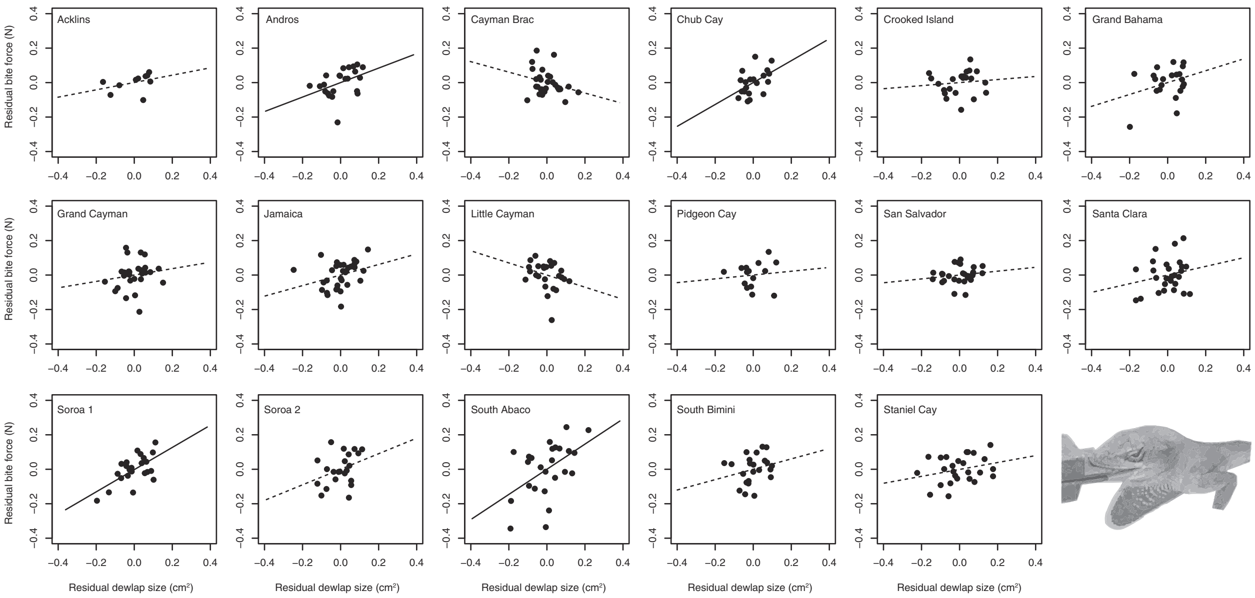


Fig. 2 Relative bite force regressed against relative dewlap size for each *A. sagrei* population, separately. Straight regression lines represent a significant correlation between both variables, i.e., Andros, Chub Cay, Soroa 1, and South Abaco. Dotted regression lines represent no significant relationship between relative dewlap size and bite force. Detailed statistics are provided in Table 2. The illustration (right, below) visualizes a male brown anole biting on a purpose-built force plate.

Table 1 Descriptive statistics of the tested variables

Populations	HL (mm)	SVL (mm)	Dewlap size (cm^2)	Bite force (N)	SSD	DI
Acklins	15.09 ± 1.06 (10)	56.36 ± 5.24 (10)	2.58 ± 0.68 (10)	5.75 ± 1.45 (10)	1.43 (10, 12)	—
Andros	12.81 ± 0.87 (23)	46.37 ± 3.25 (23)	1.21 ± 0.33 (23)	1.90 ± 0.51 (23)	1.23 (23, 18)	—
Cayman Brac	15.19 ± 1.03 (28)	55.07 ± 4.30 (28)	1.53 ± 0.39 (28)	5.22 ± 1.65 (28)	1.33 (28, 29)	0.01 ± 0.03 (23)
Chub Cay	13.92 ± 0.88 (20)	47.87 ± 3.62 (20)	1.67 ± 0.49 (20)	3.36 ± 0.92 (20)	1.32 (20, 16)	—
Crooked Island	13.68 ± 1.04 (23)	49.86 ± 4.61 (23)	1.81 ± 0.61 (23)	3.66 ± 1.34 (23)	1.25 (23, 20)	—
Grand Bahama	12.82 ± 1.43 (24)	46.78 ± 6.34 (24)	1.59 ± 0.41 (21)	2.26 ± 1.39 (24)	1.33 (24, 11)	—
Grand Cayman	14.47 ± 1.21 (27)	51.74 ± 4.57 (27)	1.64 ± 0.41 (27)	6.11 ± 2.19 (27)	1.28 (27, 29)	0.07 ± 0.11 (24)
Jamaica	13.92 ± 1.00 (32)	48.60 ± 3.98 (32)	1.17 ± 0.27 (32)	6.90 ± 2.17 (32)	1.24 (32, 23)	0.02 ± 0.03 (22)
Little Cayman	15.17 ± 1.06 (28)	53.46 ± 4.35 (28)	2.00 ± 0.56 (28)	5.22 ± 1.57 (27)	1.29 (28, 27)	0.01 ± 0.01 (23)
Pidgeon Cay	14.15 ± 0.80 (16)	48.19 ± 3.28 (16)	1.56 ± 0.39 (16)	2.82 ± 0.79 (16)	1.21 (16, 8)	—
San Salvador	16.27 ± 1.52 (27)	58.13 ± 5.85 (27)	1.96 ± 0.75 (27)	7.99 ± 2.24 (27)	1.35 (27, 14)	0.02 ± 0.02 (24)
Santa Clara	15.80 ± 0.82 (27)	55.21 ± 2.97 (27)	2.06 ± 0.36 (27)	7.68 ± 1.78 (27)	1.33 (27, 24)	0.18 ± 0.13 (24)
Soroa 1	14.84 ± 1.35 (23)	51.10 ± 4.44 (23)	1.91 ± 0.45 (23)	6.63 ± 1.94 (23)	1.24 (23, 21)	0.11 ± 0.11 (24)
Soroa 2	15.50 ± 1.03 (22)	55.45 ± 4.46 (22)	2.27 ± 0.46 (22)	7.53 ± 2.00 (22)	1.32 (22, 24)	0.17 ± 0.14 (30)
South Abaco	13.07 ± 1.16 (26)	46.59 ± 4.15 (26)	1.35 ± 0.48 (26)	2.27 ± 0.96 (25)	1.28 (26, 21)	0.02 ± 0.04 (21)
South Bimini	14.91 ± 1.38 (24)	53.66 ± 4.60 (27)	1.62 ± 0.45 (26)	4.04 ± 1.13 (24)	1.30 (27, 23)	0.02 ± 0.02 (20)
Staniel Cay	13.86 ± 1.16 (26)	51.82 ± 5.41 (26)	1.91 ± 0.69 (26)	3.14 ± 1.05 (26)	1.32 (26, 20)	—

Notes: Population means ± standard deviations are presented for each population, with the exception of SSD (i.e., mean SVL males divided by mean SVL females). Sample sizes are provided between brackets for each variable separately; for SSD the number of implemented males and females is shown (left and right, respectively). HL, head length; SVL, snout-to-vent length; SSD, sexual size dimorphism; DI, display intensity, as the proportion of time that individuals spent displaying.

size as a predictor for bite performance in a territorial Caribbean anole, and how this dewlap size–bite force relationship varies so drastically among populations. We used absolute and relative indices to assess the link between dewlap size and bite force, as both indices can differ in the messages they convey (Lailvaux and Irschick 2007).

Table 2 Univariate linear regression analyses of bite force (dependent variable) against dewlap size (independent variable) within population

Population	*R*	*F*	df	Coefficient *b* ± SE	*P*-value
Absolute bite force against dewlap size					
Acklins	0.819	16.28	9	0.761 ± 0.189	**0.004**
Andros	0.806	38.81	22	0.758 ± 0.122	**<0.001**
Cayman Brac	0.652	19.28	27	0.792 ± 0.180	**<0.001**
Chub Cay	0.909	85.16	19	0.948 ± 0.102	**<0.001**
Crooked Island	0.810	40.09	22	0.828 ± 0.131	**<0.001**
Grand Bahama	0.723	20.82	20	1.503 ± 0.329	**<0.001**
Grand Cayman	0.784	39.87	26	0.156 ± 0.183	**<0.001**
Jamaica	0.740	36.31	31	0.933 ± 0.155	**<0.001**
Little Cayman	0.704	23.55	25	0.682 ± 0.141	**<0.001**
Pidgeon Cay	0.708	14.03	15	0.622 ± 0.166	**0.002**
San Salvador	0.904	112.0	26	0.637 ± 0.060	**<0.001**
Santa Clara	0.375	4.093	26	0.471 ± 0.233	0.054
Soroa 1	0.870	65.69	22	1.078 ± 0.133	**<0.001**
Soroa 2	0.795	34.45	21	1.254 ± 0.214	**<0.001**
South Abaco	0.762	31.89	24	0.936 ± 0.166	**<0.001**
South Bimini	0.729	23.77	22	0.670 ± 0.137	**<0.001**
Staniel Cay	0.799	42.48	25	0.651 ± 0.100	**<0.001**
Relative bite force against relative dewlap size					
Acklins	0.380	1.352	9	0.214 ± 0.184	0.278
Andros	0.413	4.328	22	0.420 ± 0.202	**0.050**
Cayman Brac	0.266	1.972	27	−0.303 ± 0.216	0.172
Chub Cay	0.490	5.679	19	0.635 ± 0.267	**0.028**
Crooked Island	0.108	0.249	22	0.089 ± 0.178	0.623
Grand Bahama	0.305	1.955	20	0.345 ± 0.246	0.178
Grand Cayman	0.153	0.603	26	0.185 ± 0.239	0.445
Jamaica	0.312	3.230	31	0.306 ± 0.170	0.082
Little Cayman	0.273	1.937	25	−0.353 ± 0.254	0.177
Pidgeon Cay	0.221	0.720	15	0.186 ± 0.219	0.411
San Salvador	0.166	0.707	26	0.112 ± 0.134	0.411
Santa Clara	0.212	1.177	26	0.251 ± 0.232	0.288
Soroa 1	0.623	13.36	22	0.639 ± 0.175	**0.001**
Soroa 2	0.335	2.523	21	0.451 ± 0.284	0.128
South Abaco	0.495	7.460	24	0.729 ± 0.267	**0.012**
South Bimini	0.243	1.318	22	0.301 ± 0.262	0.264
Staniel Cay	0.271	1.907	25	0.198 ± 0.144	0.180

Notes: Results are shown for regressions with absolute and relative variables, respectively. Significant results ($P < 0.05$) are shown in bold font.

Absolute dewlap size–bite force relationship

Our results revealed that dewlap size is an excellent predictor of bite force capacity in nearly all study populations. A strong association between absolute dewlap size and bite force in *A. sagrei* males has also been reported in all previous studies (Lailvaux and Irschick 2007; Cox et al. 2009; Driessens et al. 2015), emphasizing the generality of this finding. In many animal species, including *A. sagrei*, body size is the key predictor in determining combat outcome, with larger individuals having a substantial advantage over smaller ones (e.g., Tokarz 1985; Hughes 1996; Hardy and Briffa 2013). Gathering accurate information on the opponent's body size (assessment game) seems thus crucial to avoid costs associated with escalated fights (Andersson 1994; Emlen 2008). Yet, in reality, the accurate transmission of information is often impeded by ambient noise (e.g., precipitation, low light levels, and windblown vegetation), and particularly when only one signal component is involved (e.g., Fleishman 1992; Lengagne and Slater 2002; Peters and Evans 2003; Leonard and Horn 2005). A commonly adopted signaling strategy to cope with such impeding factors is to repeat the same message in different ways by using redundant signal components (e.g., Zuk et al. 1992; Møller and Pomiankowski 1993; Johnstone 1996). Within all our study populations, absolute dewlap size correlated strongly with overall body size and might as such, serve as a redundant signal for body size to increase signal accuracy during mate assessment. Characterized by a brown to grayish body color, *A. sagrei* is well camouflaged in the microhabitats it usually occupies (trunk-ground ecomorph; Schoener and Schoener 1982; Losos 2009). In contrast, its bright yellow to reddish dewlap is highly conspicuous, due to high color and pattern contrasts with background vegetation (Endler 1992, 1993, 2012). Thus, by using the combination of a more cryptic body together with a conspicuous dewlap, males can transmit more accurate information on size and consequently, fighting capacity to opponents. The potential role of the *A. sagrei* dewlap as redundant signal for body size might be most prominent during the early stages of opponent assessment, when signaling still occurs over relatively long distances (more ambient noise), or perhaps during territorial advertisement in order to discourage unseen rival males from intruding (McMann 1998; Orrell and Jenssen 2003). Accordingly, Henningsen and Irschick (2012) showed in their study that surgically reducing the size of the dewlap did not change the outcome of staged close-proximity interactions between size-matched *A. carolinensis* males; bite force capacity in itself appeared to be more important in determining the outcome of these staged interactions. Based on their results, the authors suggested that dewlap size functions as a signal of bite force primarily during non-directed, long-distance territorial displays, whereas more direct means of assessing one another (e.g., jaw size, head size, body condition, push-ups) may be of higher importance during close-proximity aggressive interaction. In this respect, future behavioral experiments on *A. sagrei* testing the importance of absolute dewlap size as a redundant signal for size during long-distance versus short-distance male interactions might be a valuable addition.

Relative dewlap size–bite force relationship

In addition to conveying information on body size, a sexual trait can function as direct, honest signal for advertising fighting capacity (e.g., Panhuis and Wilkinson 1999; Lailvaux et al. 2005). Evidence for a positive link between relative male dewlap size and bite force during the breeding season has been shown for several territorial anole species (Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007). Surprisingly, earlier studies did not observe this correlation in the highly territorial brown anole lizard, *A. sagrei* (Lailvaux and Irschick 2007; Cox et al. 2009; Driessens et al. 2015). By examining a large set of island populations, we now also found support for a significant relationship between relative dewlap size and bite force within *A. sagrei*, though, only in 4 out of the 17 tested populations. In contrast to our expectations, the degree of SSD and DI could not explain the observed variation in the relative dewlap size–bite force relationship found among our populations. Thus, populations where relative dewlap size appeared to be an honest signal of bite force were not *per se* characterized by a higher degree of intrasexual selection, which is inconsistent to earlier findings from Lailvaux and Irschick (2007) (at the species level). Standard errors of the estimated slopes for the relative dewlap size–bite force relationships fell within a relatively narrow range (0.134–0.284, Table 2), and we therefore believe that our failure to find an association between the slopes and SSD or DI is due to the low among-population differences in variance. Another potential reason why we fail to find an association might be due to relative low sample sizes. While the majority of regression analyses showed a high statistical power (power > 0.99), hence, adequate sample sizes, analyses on the populations where relative bite force was not significantly correlated with relative dewlap size were characterized by a relative low statistical power (power < 0.5). Although our sample sizes and statistical power were similar to those of other studies that correlated relative bite force with relative dewlap size (i.e., Vanhooydonck et al. 2005a; Lailvaux and Irschick 2007; Cox et al. 2009), an increase in sample size would have increased the power of our analyses, hence, might have affected our results on an association between the slopes and SSD or DI. Moreover, one can also question the validity of SSD as a measure of the intensity of intrasexual selection. Indeed, it has long been pointed out that SSD may also arise as a consequence of natural selection for reduction of food competition (Darwin 1871) or on clutch size in females (Tinkle et al. 1970). Reassuringly, several studies have found that among-species variation in SSD correlates positively with other aspects of sexual dimorphism (such as dichromatism: Pérez I de Lanuza et al. 2013; Chen et al. 2012; Dale et al. 2015), indicating that SSD is at least to some extent under sexual selection. In a comparative analysis of almost 500 lizard species, Cox et al. (2003) did find significant correlations between SSD and female home range ratio and female home range size, two widely accepted proxies for the strength of intrasexual selection. In *Anolis*, the use of SSD as an indirect measure of sexual selection intensity has a long tradition (e.g., Trivers 1976; Stamps 1983), although several studies have suggested that variation in SSD may be driven by natural selection as well (e.g., Rand 1967; Losos et al. 2003). In a recent study on our study species *A. sagrei*, for example, Bonneaud et al. (2016) reported that resource availability can highly influence the degree of SSD among insular populations distributed across the Bahamas. Furthermore, paternity studies on *A. sagrei* proved that sexual selection is not uniformly directional with respect to male size and, therefore, fails to fully explain the observed male-biased SSD (Calsbeek and Sinervo 2004; Cox et al. 2007). Thus, the use of SSD here as metric for sexual selection is disputable. Besides, DI may be a rather "gross" proxy for the degree of intrasexual selection on each island population, because *A. sagrei* males may exhibit displays in various contexts (Driessens et al. 2014). Clearly, data on reliable estimates of the intensity of sexual selection are required. Some authors have advocated the use of sex ratios (e.g., Stamps 1983; Muralidhar and Johnson 2017), but others have warned that it is unsure to what extent observed sex ratio reflects operational sex ratio (the ratio of breeding males to breeding females, Cox et al. 2003). Other options include behavioral observations (e.g., number or duration of male–male aggressive interactions) and distributional data (territory size, overlap, number of females per territory, encounter rates; Johnson et al. 2009; Kamath and Losos 2018), but obtaining such data for many populations requires substantial time and effort, which probably explains why, after 50 years of research on anoles, such data remain largely unavailable (Losos et al. 2003).

SSD and DI cannot explain differences in the relationship between relative dewlap size and bite force among populations, but what other factors potentially can? One possible explanatory factor may involve intrapopulational variation in body size and the idea that relative indices become particularly important in populations where opponents match more often in body size. Transferring information on body size is likely the first and most crucial step in the assessment game (e.g., Tokarz 1985; Hardy and Briffa 2013), as we already stated in the previous paragraph. However, when males of similar body size encounter each other, dewlap size might become the major signal for advertising fighting capacity. In support of this idea, we would expect relative dewlap size to become a more reliable signal of bite force when variation in body size decreases across populations. We could simply test this prediction with available data by regressing the slope of the relative dewlap size–bite force relationship against variance in body size across populations. Our data did not support the proposed idea (pgls regression: coefficient b variance SVL, $R = 0.26$, df = 16, $P = 0.317$), perhaps because encounters between size-matched opponents may not occur that frequently. Moreover, previous studies have shown that when opponents are more similar in size, fights are more likely to escalate (as opposed to merely opponent assessment) and the outcomes harder to predict (Rand 1967; Molina-Borja et al. 1998; Panhuis and Wilkinson 1999). This might challenge the view that honest signals play a major role in the advertisement of fighting capacity during agonistic encounters between size-matched males.

Another factor that has recently been reported to affect the relationship between relative dewlap size and bite force is resource availability. Particularly, Lailvaux et al. (2012) showed that under limiting resource conditions, the honest dewlap size–bite force relationship in *A. carolinensis* gets disrupted. To put this idea to the test, we assessed whether variation in body condition (an estimate for resource availability) could explain the variation in the relative dewlap size–bite force relationship observed within *A. sagrei*. Indeed, we obtained a significant association with body condition (pgls regression: coefficient $b \sim$ body mass normalized for SVL, $R = 0.62$, df = 16, $P = 0.009$). However, the correlation was negative and, therefore, opposes the findings reported by Lailvaux et al. (2012). We found that for *A. sagrei* males, dewlap size in itself becomes a more reliable signal of bite force in populations where males are in worse body condition (the relationship with body condition was not significant when using the absolute dewlap size–bite force relationships, $P = 0.575$). Overall, we suggest that body size remains, independent of resource availability, the key predictor during opponent assessment. Yet, when males of similar body size encounter each other, the use of dewlap size to honestly signal fighting capacity might be particularly important for *A. sagrei* males in poor body condition. We believe that males in poor body condition will suffer more from the exhaustion and injuries related to physical fights than *A. sagrei* males in normal or good body condition. Accordingly, in populations where males have a low body condition, the strong need to avoid escalated fights and thus, to precisely assess a size-matched opponent, might be higher (Andersson 1994; Maynard-Smith and Harper 2003). This may explain why dewlap size becomes a more reliable predictor of bite force in such populations. In contrast, males under high resource conditions might directly engage in physical fights when encountering a size-matched opponent (Rand 1967; Molina-Borja et al. 1998). Of course, future experiments are needed to confirm our suggestions and to provide additional evidence that resource availability, indeed, influences the correlation between relative dewlap size and bite force in *A. sagrei*.

Last, several other factors have been found to explain variation only in dewlap size and can as such, also affect the relation between signal size and performance trait. For example, Vanhooydonck et al. (2009) revealed that *A. sagrei* males had relatively larger dewlaps in populations where curly-tailed lizards (*Leiocephalus carinatus*), known to predate on anoles, are present. In that same study was also reported that relative dewlap size increased with SSD. Also hormone levels (i.e., testosterone) are proven to change dewlap size in *A. sagrei* males (Cox et al. 2009) and can, due to fluctuating levels, affect the relationship between dewlap size and bite force throughout seasons. In accordance, a previous study on *A. carolinensis* has shown that dewlap size is only a reliable signal of bite force during the breeding season, and not during winter (Irschick et al. 2006). Following Lailvaux and Irschick (2007), we sampled our *A. sagrei* populations during the breeding season, with the exception of one (i.e., population from San Salvador). Results from that latter population did not markedly deviate from the other study populations, indicating that the dewlap–bite force relationship in *A. sagrei* might not be significantly affected by season. Yet, experiments assessing the link between dewlap size and bite force in the same *A. sagrei* individuals throughout the year are needed to accurately assess seasonal effects.

Conclusion

To our knowledge, this is the first study showing evidence for a link between relative dewlap size and bite force within *A. sagrei* populations, during the breeding season. Based on our results, we suggest that dewlap size in *A. sagrei* males is in general a redundant signal for body size in the advertisement of fighting capacity (absolute indices), but only in particular cases a direct signal of bite force (relative indices). Our study makes an important contribution by showing that the relationship between signal size and performance trait can differ substantially within one species. We therefore suggest that the use of only one population is not sufficient to draw general conclusions for a whole species, in this respect. Several factors (e.g., degree of territoriality, resource availability, season) are already known to affect the correlation between dewlap size and bite force; however, additional research is needed to shed more light on how these factors exactly affect this relationship.

Acknowledgments

We acknowledge S. De Decker, J. Harvey, A. Herrel, J. Husak, P. Maillis, J. Mertens, J.J. Meyers, D. Norris, V. Rivalta, L. Schettino, E. Schramme, B. Scott-Edwards, M. Valley, and L. Vandervorst for help during data collection. We further thank G. Reynolds for his useful advice regarding phylogenetic analyses, S. Van Dongen for statistical assistance, and two anonymous reviewers for significantly improving drafts of this manuscript.

Funding

This work was supported by the Belgian American Education Foundation (BAEF) [to S.B. a postdoctoral fellow]. This study was financed by an FWO-FL research grant [to T.D., an aspirant doctoral fellowship]. K.H. is a postdoctoral fellow of FWO-FL. Additional expenses for field missions were provided by Leopold III fund and the University of Antwerp (DOCOP). All work was carried out in accordance with the local Environmental Agencies and the University of Antwerp animal welfare standard and protocols (ECD 2011-64).

References

Abe J, Kamimura Y, Kondo N, Shimada M. 2003. Extremely female-biased sex ratio and lethal male–male combat in a parasitoid wasp, *Melittobia australica* (Eulophidae). Behav Ecol 14:34–9.

Alonso-Alvarez C, Bertrand S, Devevey G, Gaillard M, Prost J, Faivre B, Sorci G. 2004. An experimental test of the dose-dependent effect of carotenoids and immune activation on sexual signals and antioxidant activity. Am Nat 164:651–9.

Anderson RA, McBrayer LD, Herrel A. 2008. Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. Biol J Linn Soc 93:709–20.

Andersson M. 1982. Female choice selects for extreme tail length in a widowbird. Nature 299:529–34.

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press. 624 p.

Baeckens S, Driessens T, Van Damme R. 2016. Intersexual chemo-sensation in a "visually-oriented" lizard, *Anolis sagrei*. PeerJ 4:e1874.

Baeckens S, García-Roa R, Martín J, Ortega J, Huyghe K, Van Damme R. 2017. Fossorial and durophagous: implications of molluscivory for head size and bite capacity in a burrowing worm lizard. J Zool 301:193–205.

Bean D, Cook JM. 2001. Male mating tactics and lethal combat in the nonpollinating fig wasp *Sycoscapter australis*. Anim Behav 62:535–42.

Bels V. 1990. The mechanism of dewlap extension in *Anolis carolinensis* (Reptilia: iguanidae) with histological analysis of the hyoid apparatus. J Morphol 206:225–44.

Bennett AF. 1985. Temperature and muscle. J Exp Biol 155:333–44.

Blomberg SP, Garland T, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–45.

Blumstein DT, Daniel JC. 2007. Quantifying behavior the JWatcher way. Sunderland (MA): Sinauer Associates. 211 p.

Bonneaud C, Marnocha E, Herrel A, Vanhooydonck B, Irschick DJ, Smith TB. 2016. Developmental plasticity affects sexual size dimorphism in an anole lizard. Funct Ecol 30:235–43.

Bradbury JW, Vehrencamp SL. 1998. The principles of animal communication. Sunderland (MA): Sinauer Associates. 697 p.

Butler MA, Sawyer SA, Losos JB. 2007. Sexual dimorphism and adaptive radiation in *Anolis* lizards. Nature 447:202–5.

Calsbeek R, Sinervo B. 2004. Progeny sex is determined by relative male body size within polyandrous females' clutches: cryptic mate choice in the wild. J Evol Biol 17:464–70.

Candolin U. 2003. The use of multiple cues in mate choice. Biol Rev 78:575–95.

Carpenter CC. 1978. Ritualistic social behaviors in lizards. In: Greenberg N, MacLean PD, editors. Behavior and neurology of lizards. Rockville (MD): NIMH. p. 253–67.

Chen IP, Stuart-Fox D, Hugall AF, Symonds MRE. 2012. Sexual selection and the evolution of complex color patterns in dragon lizards. Evolution 66:3605–14.

Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus L.*) Anim Behav 27:211–25.

Cox RM, Skelly SL, John-Alder HB. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57:1653–69.

Cox RM, Butler MA, John-Alder HB. 2007. The evolution of sexual size dimorphism in reptiles. In: Fairbairn DJ, Blanckenhorn WU, Szekely T, editors. Sex, size & gender roles: evolutionary studies of sexual size dimorphism. Oxford: Oxford University Press. p. 38–49.

Cox RM, Stenquist DS, Henningsen JP, Calsbeek R. 2009. Manipulating testosterone to assess links between behavior, morphology, and performance in the brown anole *Anolis sagrei*. Physiol Biochem Zool 82:686–98.

Crews D. 1975. Effects of different components of male courtship behavior on environmentally induced ovarian recrudescence and mating preferences in the lizard *Anolis carolinensis*. Anim Behav 23:349–56.

Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu M. 2015. The effects of life history and sexual selection on male and female plumage colouration. Nature 527:367–70.

Darwin CR. 1871. The descent of man, and selection in relation to sex. London: John Murray. 745 p.

Driessens T, Vanhooydonck B, Damme R. 2014. Deterring predators, daunting opponents or drawing partners? Signaling rates across diverse contexts in the lizard *Anolis sagrei*. Behav Ecol Sociobiol 68:173–84.

Driessens T, Huyghe K, Vanhooydonck B, Van Damme R. 2015. Messages conveyed by assorted facets of the dewlap, in both sexes of *Anolis sagrei*. Behav Ecol Sociobiol 69:1251–64.

Driessens T, Baeckens S, Balzarolo M, Vanhooydonck B, Huyghe K, Van Damme R. 2017. Climate-related environmental variation in a visual signalling device: the male and female dewlap in *Anolis sagrei* lizards. J Evol Biol 30:1846–61.

Edwards JR, Lailvaux SP. 2012. Display behavior and habitat use in single and mixed populations of *Anolis carolinensis* and *Anolis sagrei* lizards. Ethology 118:494–502.

Emlen DJ. 2008. The evolution of animal weapons. Annu Rev Ecol Evol 39:387–413.

Endler JA. 1992. Signals, signal conditions, and the direction of evolution. Am Nat 139:125–53.

Endler JA. 1993. The color of light in forests and its implications. Ecol Monogr 63:1–27.

Endler JA. 2012. A framework for analysing colour pattern geometry: adjacent colours. Biol J Linn Soc 107:233–53.

Felsenstein LJ. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Fleishman LJ. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. Am Nat 139:36–61.

Garland T, Ives AR. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. Am Nat 155:346–64.

Greenberg G, Noble GK. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voigt). Physiol Zool 17:392–439.

Hardy ICW, Briffa M. 2013. Animal contests. Cambridge (MA): Cambridge University Press. 379 p.

Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press. 248 p.

Henningsen JP, Irschick DJ. 2012. An experimental test of the effect of signal size and performance capacity on dominance in the green anole lizard. Funct Ecol 26:3–10.

Herrel A, O'Reilly JC. 2006. Ontogenetic scaling of bite force in lizards and turtles. Physiol Biochem Zool 79:31–42.

Herrel A, Spithoven L, Van Damme R, De Vree F. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. Funct Ecol 13:289–97.

Herrel A, Aerts P, Fret J, De Vree F. 1999. Morphology of the feeding system in agamid lizards: ecological correlates. Anat Rec 254:496–507.

Herrel A, Van Damme R, Vanhooydonck B, De Vree F. 2001. The implications of bite performance for diet in two species of lacertid lizards. Can J Zool 79:662–70.

Hertz PE, Huey RB, Stevenson RD. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am Nat 142:796–818.

Huey RB. 1982. Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH, editors. Biology of the reptilia. New York (NY): Academic Press. p. 25–91.

Hughes M. 1996. Size assessment via a visual signal in snapping shrimp. Behav Ecol Sociobiol 38:51–7.

Irschick DJ, Ramos M, Buckley C, Elstrott J, Carlisle E, Lailvaux SP, Bloch N, Herrel A, Vanhooydonck B. 2006. Are morphology–performance relationships invariant across different seasons? A test with the green anole lizard (*Anolis carolinensis*). Oikos 114:49–59.

Jennions MD, Backwell PRY. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. Biol J Linn Soc 57:293–306.

Jenssen TA. 1970. The ethoecology of *Anolis nebulosus*. J Herpetol 4:1–38.

Jenssen TA, Greenberg N, Hovde KA. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. Herpetol Monogr 9:41–62.

Jenssen TA, Lovern M, Congdon JD. 2001. Fieldtesting the protandry-based mating system for the lizard *Anolis carolinensis*: does the model organism have the right model? Behav Ecol Sociobiol 50:162–72.

Johnson MA, Wade J. 2010. Behavioural display systems across nine *Anolis* lizard species: sexual dimorphisms in structure and function. Proc R Soc B Biol Sci 277:1711–9.

Johnson MA, Revell LJ, Losos JB. 2009. Behavioral convergence and adaptive radiation: effects of habitat use on territorial behavior in *Anolis* lizards. Evolution 64:1151–9.

Johnstone RA. 1996. Multiple displays in animal communication: "backup signals" and "multiple messages". Philos Trans R Soc B 351:329–38.

Kamath A, Losos JB. 2017. The erratic and contingent progression of research on territoriality: a case study. Behav Ecol Sociobiol 71:1–13.

Kamath A, Losos JB. 2018. Estimating encounter rates as the first step of sexual selection in the lizard *Anolis sagrei*. Proc R Soc B Biol Sci 285:20172244.

Kamilar JM, Cooper N. 2013. Phylogenetic signal in primate behavior, ecology and life history. Philos Trans R Soc B 368:20120341.

Karsten KB, Andriamandimbiarisoa LN, Fox SF, Raxworthy CJ. 2009. Sexual selection on body size and secondary sexual characters in 2 closely related, sympatric chameleons in Madagascar. Behav Ecol 20:1079–88.

Lailvaux SP, Irschick DJ. 2007. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. Am Nat 170:573–86.

Lailvaux SP, Herrel A, Vanhooydonck B, Meyers JJ, Irschick DJ. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). Proc R Soc B Biol Sci 271:2501–8.

Lailvaux SP, Hathway J, Pomfret J, Knell RJ. 2005. Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: scarabaeidae). Funct Ecol 19:632–9.

Lailvaux SP, Gilbert RL, Edwards JR. 2012. A performance-based cost to honest signalling in male green anole lizards (*Anolis carolinensis*). Proc R Soc B Biol Sci 279:2841–8.

Lailvaux SP, Leifer J, Kircher BK, Johnson MA. 2015. The incredible shrinking dewlap: signal size, skin elasticity, and mechanical design in the green anole lizard (*Anolis carolinensis*). Ecol Evol 5:4400–9.

Lappin AK, Husak JF. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). Am Nat 166:426–36.

Leal M, Rodríguez-Robles JA. 1995. Antipredator responses of *Anolis cristatellus* (Sauria: polychrotidae). Copeia 1995:155–61.

Leal M, Rodríguez-Robles JA. 1997. Signaling displays during predator–prey interactions in a Puerto Rican anole, *Anolis cristatellus*. Anim Behav 54:1147–54.

Lee JC, Clayton D, Eisenstein S, Perez I. 1989. The reproductive cycle of Anolis sagrei in southern Florida. Copeia 1989:930–7.

Leimar O, Austad S, Enquist M. 1991. A test of the sequential assessment game: fighting in the bowl and doily spider *Frontinella pyramitela*. Evolution 45:862–74.

Lengagne T, Slater PJB. 2002. The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. Proc R Soc Lond B 269:2121–5.

Leonard ML, Horn AG. 2005. Ambient noise and the design of begging signals. Proc R Soc B Biol Sci 272:651–6.

Losos JB. 1985. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. Copeia 4:905–10.

Losos JB, Butler M, Schoener TW. 2003. Sexual dimorphism in body size and shape in relation to habitat use among species of Caribbean *Anolis* lizards. In: Fox SF, McCoy, JKBaird TA, editors. Lizard social behaviour. Baltimore: John Hopkins University Press. p. 356–380.

Losos JB. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of Anoles. Berkeley (CA): University of California Press. p. 528.

Maynard-Smith J, Harper D. 2003. Animal signals: Oxford series in ecology and evolution. New York: Oxford University Press. p. 1–166.

McMann S. 1998. Display behavior and territoriality in the lizard *Anolis sagrei* [PhD dissertation]. University of Miami (FL).

McMann S. 2000. Effects of residence time on displays during territory establishment in a lizard. Anim Behav 59:513–22.

Molina-Borja M, Padron-Fumero M, Alfonso-Martin T. 1998. Morphological and behavioral traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (family Lacertidae). Ethology 104:314–22.

Møller AP, Pomiankowski A. 1993. Why have birds got multiple sexual ornaments. Behav Ecol Sociobiol 32:167–76.

Muralidhar P, Johnson MA. 2017. Sexual selection and sex ratios in Anolis lizards. J Zool 302:178–83.

Nicholson KE, Harmon LJ, Losos JB. 2007. Evolution of *Anolis* lizard dewlap diversity. PLoS One 2:e274.

Ord TJ, Blumstein DT, Evans CS. 2001. Intrasexual selection predicts the evolution of signal complexity in lizards. Proc R Soc B Biol Sci 268:737–44.

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2013. Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2 (https://cran.r-project.org/web/packages/caper/; last accessed November 2017).

Orrell KS, Jenssen TA. 2003. Heterosexual signaling by the lizard Anolis carolinensis, with intersexual comparisons across contexts. Behaviour 140:603–34.

Panhuis TM, Wilkinson GS. 1999. Exaggerated eye span influences male contest outcome in stalk-eyed flies. Behav Ecol Sociobiol 46:221–7.

Pérez I de Lanuza G, Font E, Monterde EL. 2013. Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. J Evol Biol 26:1826–35.

Perry G, Levering K, Girard I, Garland T. 2004. Locomotor performance and dominance in male *Anolis cristatellus*. Anim Behav 67:37–47.

Peters RA, Evans CS. 2003. Design of the Jacky dragon visual display: signal and noise characteristics in a complex moving environment. J Comp Physiol A 189:447–59.

Rand AS. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc US Nat Mus 122:1–79.

Rand AS, Williams EE. 1970. An estimation of redundancy and information content of anole dewlaps. Am Nat 104:99–103.

Revell LJ. 2010. Phylogenetic signal and linear regression on species data. Methods Ecol Evol 1:319–29.

Schoener TW, Schoener A. 1980. Densities sex ratios and population structure in four species of Bahamian *Anolis* lizards. J Anim Ecol 49:19–54.

Schoener TW, Schoener A. 1982. The ecological correlates of survival in some Bahamanian Anolis lizards. Oikos 392:1–26.

Scott MP. 1984. Agonistic and courtship displays of male *Anolis sagrei*. Breviora 479:1–22.

Setchell JM, Wickings J. 2005. Dominance, status signals, and coloration in mandrills (*Mandrillus sphinx*). Ethology 111:25–30.

Simon V. 2011. Communication signal rates predict interaction outcome in the brown anole lizard, *Anolis sagrei*. Copeia 2011:38–45.

Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practices of statistics in biological research. New York (NY): Freeman WH. 880 p.

Stamps 1983. Sexual selection, sexual dimorphism and territoriality. In. Pianka ER, Schoener TW, editors. Lizard ecology: studies of a model organism. Cambridge (MA): Harvard University Press. p. 169–204.

Stamps JA, Losos JB, Andrews RM. 1997. A comparative study of population density and sexual size dimorphism in lizards. Am Nat 149:64–90.

Steffen JE, Guyer CC. 2014. Display behaviour and dewlap colour as predictors of contest success in brown anoles. Biol J Linn Soc 111:646–55.

Tinkle DW, Wilbur HM, Tilley SG. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

Tokarz RR. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Anim Behav 33:746–53.

Tokarz RR. 1987. Effects of cortisone treatment on male aggressive behavior in a lizard (*Anolis sagrei*). Horm Behav 21:358–70.

Tokarz RR. 1998. Mating pattern in the lizard, *Anolis sagrei*: implications for mate choice and sperm competition. Herpetologica 54:388–94.

Tokarz RR. 2002. An experimental test of the importance of the dewlap in male mating success in the lizard *Anolis sagrei*. Herpetologica 58:87–94.

Tokarz RR, Paterson AV, McMann S. 2003. Laboratory and field test of the functional significance of the male's dewlap in the lizard *Anolis sagrei*. Copeia 2003:502–11.

Trivers RL. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:253–69.

Vanhooydonck B, Herrel A, Van Damme R, Irschick DJ. 2005a. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? Funct Ecol 19:38–42.

Vanhooydonck B, Herrel A, Van Damme R, Meyers JJ, Irschick DJ. 2005b. The relationship between dewlap size and performance changes with age and sex in a Green Anole (*Anolis carolinensis*) lizard population. Behav Ecol Sociobiol 59:157–65.

Vanhooydonck B, Herrel A, Meyers JJ, Irschick DJ. 2009. What determines dewlap diversity in *Anolis* lizards? An among-island comparison. J Evol Biol 22:293–305.

Zuk M, Ligon JD, Thornhill R. 1992. Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. Anim Behav 44:999–1006.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 38–51
doi:10.1093/icb/icy018

Society for Integrative and Comparative Biology

INVITED PERSPECTIVES

Leveraging Organismal Biology to Forecast the Effects of Climate Change

Lauren B. Buckley,[1] Anthony F. Cannistra and Aji John

Department of Biology, University of Washington, Seattle, WA 98195-1800, USA

[1]E-mail: lbuckley@uw.edu

Synopsis Despite the pressing need for accurate forecasts of ecological and evolutionary responses to environmental change, commonly used modeling approaches exhibit mixed performance because they omit many important aspects of how organisms respond to spatially and temporally variable environments. Integrating models based on organismal phenotypes at the physiological, performance, and fitness levels can improve model performance. We summarize current limitations of environmental data and models and discuss potential remedies. The paper reviews emerging techniques for sensing environments at fine spatial and temporal scales, accounting for environmental extremes, and capturing how organisms experience the environment. Intertidal mussel data illustrate biologically important aspects of environmental variability. We then discuss key challenges in translating environmental conditions into organismal performance including accounting for the varied timescales of physiological processes, for responses to environmental fluctuations including the onset of stress and other thresholds, and for how environmental sensitivities vary across lifecycles. We call for the creation of phenotypic databases to parameterize forecasting models and advocate for improved sharing of model code and data for model testing. We conclude with challenges in organismal biology that must be solved to improve forecasts over the next decade.

Introduction

Many organisms have responded to recent climate change by shifting their distribution or phenology, experiencing population shifts, acclimating, or evolving (Scheffers et al. 2016). Yet, we have little ability to predict how particular species will respond based on their traits (Buckley and Kingsolver 2012; MacLean and Beissinger 2017). Considering the complexities of how organisms respond to their environments and to other organisms, our poor predictive ability is not particularly surprising. Prediction is particularly challenging because organisms will increasingly experience environments that are novel with regard to their evolutionary histories (Veloz et al. 2012; Maguire et al. 2015). A core challenge is to identify which aspects of organismal biology are essential to consider and which can be omitted from predictive models.

Predicting responses to environmental change offers an opportunity to test our understanding of organismal biology. Indeed, making accurate predictions requires addressing most of the grand challenges in organismal animal biology identified by the Society for Integrative and Comparative Biology (SICB) (Schwenk et al. 2009). In particular, physiological insight is needed to integrate across levels of biological organization (Mykles et al. 2010), whether organisms use behavior to buffer their environment must be considered (Sih et al. 2010), and appropriately characterizing organism–environment interactions requires an interplay between theory and empirical research (Angilletta and Sears 2011). Robust forecasts require operationalizing knowledge gained from the grand challenges (Denny and Helmuth 2009).

Statistical environmental niche models (ENMs) remain the most common forecasting tool, but their performance is mixed (Maguire et al. 2015). For example, using ENMs to prioritize reserve design for mammals during a past period of rapid climate change yielded performance that was little better than random prioritization (Williams et al. 2013). One point of ENMs failure is poor extrapolation into novel environments (Veloz et al. 2012). Mechanistic modeling approaches that incorporate environmental data and phenotypes to estimate

Advance Access publication April 26, 2018

physiology, performance, and ultimately fitness (rather than relying on statistical associations between environmental conditions and organism presence as do ENMs) should extrapolate better into novel environments (Buckley et al. 2010; Urban et al. 2016).

Effective forecasts must address how organisms respond to spatially and temporally variable environments. Many distribution models such as ENMs can readily incorporate finer spatial data but generally require temporally averaged environmental data. They thus omit many important aspects of organismal responses including thresholds, non-linearities, and thermal histories. Mechanistic models are well suited to handle time series of environmental data, but their application is limited by the availability of biophysical models and organismal data (Helmuth et al. 2005; Buckley et al. 2010; Urban et al. 2016).

Here we summarize data and modeling limitations for ecological and evolutionary forecasting and highlight promising directions. Limitations to environmental data, and to associated climatic, biophysical, and niche models, undermine our ability to accurately forecast responses to climate change (Dillon and Woods 2016; Nadeau et al. 2017). The availability of environmental data is increasing rapidly, but they generally are not provided at the fine spatial and temporal scales relevant to the physiology, energetics, and demography of organisms (Potter et al. 2013). Limited data on morphological and physiological phenotypes (and their inter-individual and interpopulation variation) hinder modeling organismal responses to environmental conditions (Urban et al. 2016). Existing knowledge is largely inadequate to predict how organisms evade (through behavior or other forms of plasticity) or cope with environmental stresses, particularly given that the incidence and magnitude of environmental stress varies temporally.

Most of these limitations have been reviewed elsewhere (e.g., Helmuth et al. 2005; Kearney and Porter 2009; Buckley et al. 2010; Huey et al. 2012; Dillon and Woods 2016; Sinclair et al. 2016; Urban et al. 2016; Dietze et al. 2018), but we see value in a synthetic assessment of challenges for ecological and evolutionary forecasting and a roadmap for their potential remedies. We highlight recent progress toward addressing the limitations, which combined substantially enhance our forecasting capacity. We consider better leveraging organismal biology as central to meeting the remaining challenges. Our assessment concentrates on ectothermic animals for tractability, but many of the limitations are general across taxa.

We advocate integrating models at the physiological, performance, and fitness levels to connect environmental conditions, phenotypes, and the ecological and evolutionary consequences of climate change (Buckley and Kingsolver 2012). We divide our review into three sections corresponding to components of the modeling approach (Fig. 1). First, the environment must be sensed at scales relevant to organismal physiology. Second, these microclimatic conditions must be filtered through organismal phenotypes to estimate body temperature and organismal energy and water balances (Porter and Tracy 1983). These patterns can be integrated with organismal performance data to predict consequences for survival, development, and reproduction. Third, these different fitness components can be combined to predict population demography and fitness.

Sensing the environment at scales relevant to organismal physiology

Online databases and dissemination tools are rapidly expanding access to environmental data. However, few tools are equipped to deliver data with sufficiently fine spatial and temporal resolution to be immediately biologically relevant (but see our group's efforts at trenchproject.github.io). Fine scale data are also limited. Air temperature data are widely available, but estimating the body temperatures of terrestrial organisms minimally requires data on surface temperature, radiation, and wind speed and energy budget models for integrating those data. Unfortunately, temperature data tend to be available at spatial resolutions 10,000-fold coarser than the size of focal animals and 1000-fold coarser than the size of focal plants (Potter et al. 2013). Most point or interpolated data are derived from weather stations with a height of 2 m, where temperatures can be drastically different from those close to the ground, where organisms often occupy surface boundary layers (see also microclimate model section below).

Dataloggers and sensors

Many researchers try to circumvent these problems by using data loggers to collect their own microclimate data (Bramer et al. 2018). iButtons and similar sensors are relatively inexpensive and easily used to record air or water temperature. Their utility can be enhanced by embedding them in physical models of organisms or live organisms so that they indicate body temperatures (Bakken 1992; Dzialowski 2005; Helmuth et al. 2016). However, many organisms are too small to make iButtons practical.

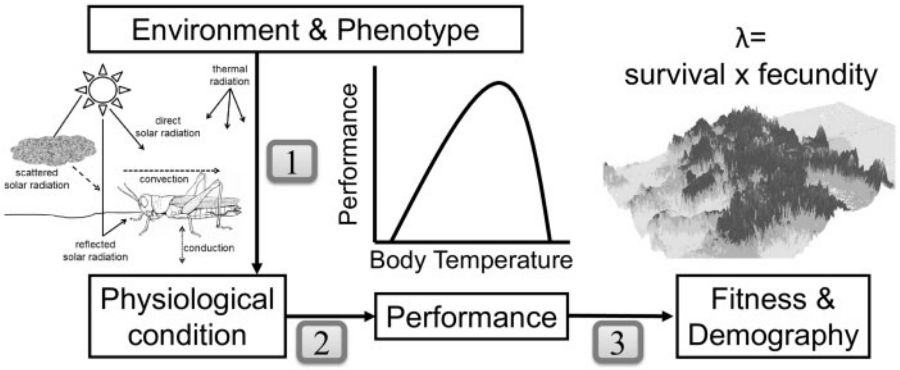


Fig. 1 An ecological forecasting framework using (1) environmental conditions and an organism's phenotype to predict its physiological condition such as heat and water balance. (2) Estimates of organismal performance as a function of physiological condition can be used to (3) predict fitness components such as survival and fecundity and ultimately demography and distributions. The numbers correspond to sections of our review.

The thermocouples or thermistors compatible with many data loggers are likewise too bulky for many small organisms. Small thermocouples or thermistors generally require channels that measure voltage or resistance levels, which can be prohibitively expensive. Single loggers with a sufficient number of channels can cost thousands of dollars, resulting in complex tangles of thermocouple or thermistor wires connecting to single data loggers. Data loggers suitable for the fine-scale measurements needed by organismal biologists remain difficult to obtain and deploy and lag far behind the technological innovations available for other applications (e.g., industrial).

Low-cost microcontrollers (e.g., the Arduino open-source electronic prototyping platform) built onto single circuit boards are rapidly expanding sensor and data logging options, but biologists often lack the electronics skills required to deploy the microcontrollers. Communities of electronic hackers (create.arduino.cc, hackster.io, instructables.com) assist aspiring creators, but easy to implement plans for environmental data loggers are needed (but see github.com/millerlp/Thermocouple_datalogger). Although low-cost solutions have improved considerably, investment of time and energy is required to make them reliable (Barnard et al. 2014). Deployment (e.g., cabling and waterproofing) and long-term viability in the field remains a challenge (Lockridge et al. 2016). Approaches for creating wireless networks of data loggers are also needed.

Sensing spatial variation: IR cameras, drones, and satellites

Low-cost, versatile data loggers promise improved spatial and temporal resolution for environmental data, but complementing dataloggers with spatial sensing tools can improve characterizations of microclimate variability across landscapes. Information on how animals use microclimate variability is also needed. As animals move through landscapes, particularly for behavioral thermoregulation, their experience of the environment can differ drastically from mean conditions (Huey et al. 2012; Potter et al. 2013; Woods et al. 2015). The spatial distribution of microclimates influences the efficacy of thermoregulation (Sears et al. 2016). Lightweight tracking devices offer information on how organisms are moving through and using microclimates (Kays et al. 2015).

Remote sensing can effectively characterize microclimate landscapes in some habitats (Anderson and Gaston 2013) but is sensitive to methodological issues such as sensing distance and differences in emissivity among organisms and surfaces (Faye et al. 2016). Remote sensing is thus particularly powerful when validated using on the ground sensors (Sutton and Lakshmi 2017). Promising technologies for assessing surface temperatures and other environmental variables include thermal cameras mounted on drones and satellites (Faye et al. 2016). Thermal cameras are becoming more affordable and accessible. Options include inexpensive cameras that attach to smartphones (e.g., FLiR one, SEEK), but they offer limited resolution and accuracy relative to more traditional thermal cameras. Additionally, few inexpensive options offer the ability to expediently extract temperatures for each pixel or to collect time series. Reduced restrictions on flying drones are expanding their use in assessing microclimate landscapes (Allan et al. 2015). Although satellite data are proliferating, many satellites do not collect appropriate thermal IR data for estimating land surface temperature. Hopefully the situation will improve as new initiatives and private companies expand data availability (Boyle et al. 2014; Turner et al. 2015).

Microclimate and biophysical models

Once fine-scale data are obtained, the challenge remains to estimate how organisms filter the microclimates into body temperatures. The challenge consists of two components: (1) estimating the microclimate experienced by organisms and (2) estimating body temperatures based on microclimate. Both empirical (sensors) and modeling tools exist to address each challenge. Sensors mimicking the physical properties of organisms (e.g., see "robomussel" section below) indicate body temperatures in particular microclimates, but have limited utility for estimating body temperatures in other sites, for other organisms, or at other times. Alternatively, models of energy fluxes within the environment (e.g., soil) or between organisms and the environment provide a general approach to predict temperatures (Kearney et al. 2014; Levy et al. 2016), but errors can be generated due to both the quality of the input environmental data and the models' approximations. We describe modeling approaches below with the hope of encouraging further development and application.

Biophysical equations have long been available to predict the microclimates and body temperatures available to organisms based on environmental data (Porter and Gates 1969; Gates 1980; Campbell and Norman 2000). Porter and colleagues have pioneered the development of biophysical models in ecology, but adoption has been limited due to model inaccessibility. Their release of the NicheMapR R package has recently expanded access to these tools (Kearney and Porter 2017), but the source code is only available for a subset of functions at this stage. Other functions are released only as Fortran executables, which limits their utility because they cannot be modified and one must rely on documentation to understand their performance. Others, including our research group (trenchproject.github.io), are working to increase the transparency and adaptability of microclimate models by releasing open-source versions.

For the first challenge component, microclimate modeling tools can simulate diurnal variation and estimate temperature and wind speed profiles, which can scale data from the measurement height (usually ~2 m) to the height relevant to organisms (Porter et al. 1973; Campbell and Norman 2000). Microclimate models can also be used to estimate unmeasured variables. For example, soil energy balances can be modeled to estimating surface and soil temperatures based on air temperature, wind speed, and radiation (Kearney and Porter 2017). Solar radiation responsible for heating organisms can be modeled, but cloudiness is an important determinant of heating and difficult to estimate (Porter and Gates 1969; Porter et al. 1973; Campbell and Norman 2000; Kearney et al. 2014; Norris et al. 2016).

For the second challenge component, energy budget models balance heat losses and gains from thermal and solar radiation, conduction with the ground, and convection with the surrounding air or water to estimate organismal body temperatures (Porter and Gates 1969; Gilman et al. 2006; Kearney and Porter 2017). The models require phenotypic data (e.g., solar and thermal absorptivity, morphology, and physical properties) in addition to environmental data. Air temperature is often used as a proxy for body temperature in climate change studies, but body temperatures can differ substantially from air temperatures for organisms that absorb solar radiation or evaporatively cool (Sunday et al. 2014). Increasing availability of biophysical modeling tools should improve estimates of how organisms experience microclimates.

Accounting for environmental variability and extremes

Most techniques for measuring and analyzing environmental variability and organismal responses have focused on mean or constant environmental conditions. Failing to consider environmental variability and extremes may compromise forecasts. The nonlinearity of biological rates, with rate increases in warm temperatures occurring faster than linear, leads mean biological rates in variable environments to differ from, and generally exceed, biological rates at mean temperatures (i.e., Jensen's inequality [Martin and Huey 2008; Denny 2017]). The asymmetry of the temperature dependence of organismal performance additionally makes accounting for environmental variability essential (Martin and Huey 2008; Huey et al. 2012; Vasseur et al. 2014; Sinclair et al. 2016).

Extreme climatic events are a biologically important component of climate variability, but their inherent rarity poses a challenge for assessing their biological relevance. Environmental statistics offers techniques for describing the incidence and magnitude of environmental extremes, but the approaches have been only sparsely applied to biology (Denny and Gaines 2002; Denny et al. 2009). Statistical distributions that depart from normality (e.g., extreme value distributions) can accurately characterize the tails of temperature distributions and improve forecasts of future extremes (Kingsolver and Buckley 2017).

Translating time series of environmental data into frequencies can aid understanding time scales of environmental variation and biological responses (Dillon et al. 2016). In addition to the challenge of quantifying environmental extremes, relatively few measurements of biological responses and rates (other than critical thermal and survival limits) are made at temperatures corresponding to the tails of distributions (Kingsolver and Buckley 2017). Quantifying responses in variable and extreme environments will be central to accurate ecological and evolutionary forecasts.

Case study: assessing environmental variability and extremes for intertidal mussels

Helmuth and colleagues have deployed an extensive network of robomussels-thermal data loggers with physical properties similar to mussels and thus with similar body temperatures. The data demonstrate the ubiquity of body temperature variation both within and among sites (Helmuth 2002; Helmuth et al. 2010, 2016). Here we leverage their published database (Helmuth et al. 2016) to illustrate the environmental variation within and among sites on the US west coast. Quantifying environmental variability and extremes can inform forecasting tools and enables generating realistic environmental data for incorporation in ecological and evolutionary forecasts.

We downloaded data for all sites in Washington, Oregon, and California from http://datadryad.org/resource/doi:10.5061/dryad.6n8kf. We analyzed all years of available data and all tidal elevations. We conducted a frequency analysis (employing the spec_lomb_phase R function available at github.com/georgebiogeekwang/tempcycles/) to analyze the amplitude of environmental variation as a function of frequency (Wang and Dillon 2014; Dillon et al. 2016). We consider a sequence of 400 frequencies ranging from 0.001 to 1 days^{-1}. Finally, we apply generalized extreme value (GEV) statistics (as in Kingsolver and Buckley 2017) to characterize the incidence of extreme thermal stress events. We fit GEV distributions to maximum daily robomussel temperatures using maximum likelihood and the gev.fit function in the ismev R package. We fit stationary distributions, but note that non-stationary fits can be used to account for shifts in the distribution due to climate change. We use the generalized Pareto distribution to characterize the tails of the distribution. We fit the distribution using maximum likelihood with the fpot function from the R package evd. Our R code is available at github.com/lbuckley/ClimateBiology.

The maximum daily temperatures of robomussels vary considerably within sites across the summer season due to microclimate differences (Fig. 2a). Local microclimates are particularly variable for intertidal mussels because heat extremes are experienced when the mussels are exposed to solar radiation during low tide. Thermal extremes depart from a typical latitudinal pattern, dramatically so because low tides tend to occur at midday in summer at the northern sites (Helmuth 2002; Helmuth et al. 2016). For example, the mid latitude site in Oregon reaches more extreme daily maxima than the southern California site (Fig. 2a). Microclimate variation is particularly pronounced for mussels due to their occupying different tidal elevations, but we note that similar vertical microclimate gradients occur in other habitats such as forests (Scheffers et al. 2014; Kaspari et al. 2015).

Employing a Fourier transform to partition the environmental variability into a sum of sine waves with different phases allows examining how the amplitude of environmental variation varies as a function of time interval (Wang and Dillon 2014; Dillon et al. 2016). Applying the analysis to robomussel data from three exemplar sites reveals that intervals of temporal variation are fairly characteristic within sites (Fig. 2b). We highlight the amplitude of variation at intervals of 1 week, 2 weeks, 1 month, and 1 year. Each of the sites exhibits extensive variation at the 2-week interval, corresponding to tidal cycles (Fig. 2b). Diurnal variation is substantial. The sites also experience pronounced interannual variation, likely reflecting regional climate oscillations.

Expanding the analysis to additional sites confirms that patterns of thermal stress depart from smooth latitudinal clines (Fig. 3). Northern sites tend to experience the most pronounced seasonal variation. While summers are generally cooler, the northern sites exhibit the warmest summer extremes due to large tidal fluctuations (Helmuth 2002; Helmuth et al. 2016).

GEV statistics can quantify the latitudinal patterns of variation (Kingsolver and Buckley 2017). GEV distributions are appropriate for distributions that depart from normality due to thick tails corresponding to a high prevalence of thermal extremes. Although GEV analyses have more frequently been applied to rare extreme events, they are increasingly being applied to daily maximum or minimum temperature data (Kingsolver and Buckley 2017). GEV distributions are described by three parameters: location indicates the position along the x axis, scale indicates the breadth, and shape indicates the

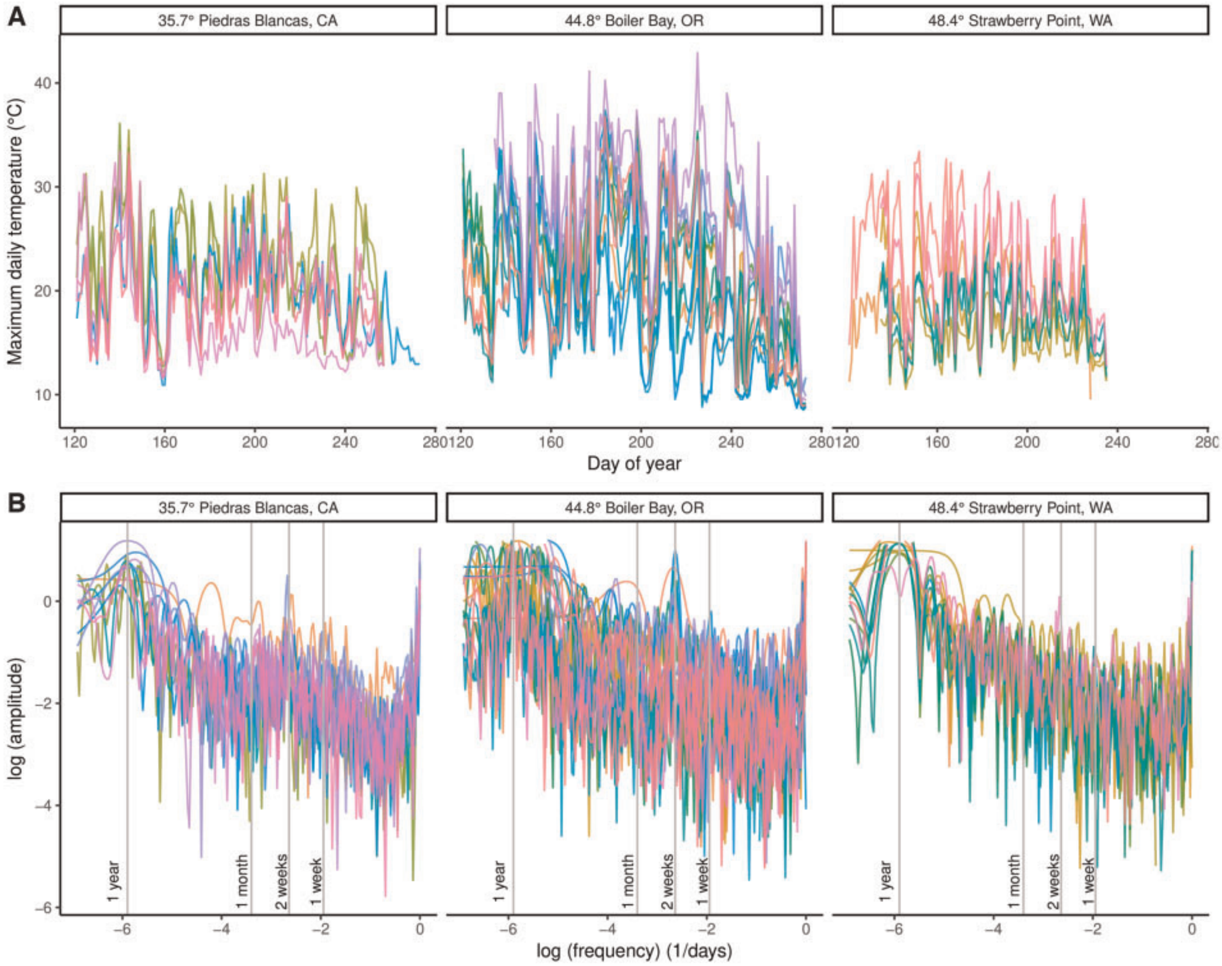


Fig. 2 (**A**) Seasonal patterns of robomussel maximum daily temperature are variable both among (column labels: site names and latitudes) and within (colors: subsites, which vary in tidal height and habitat within sites). We depict data from 2002. Thermal extremes do not follow latitudinal gradients. See huckleylab.shinyapps.io/ClimateBiology/ for an interactive version. (**B**) Patterns of temporal variability can be characterized by analyzing the amplitude of variation as a function of frequency. Vertical lines indicate intervals of (from right to left) 1 week, 2 weeks, 1 month, and 1 year.

heaviness of the tail (illustrated in Kingsolver and Buckley 2017). Fitting GEV distributions to robomussel data reveals that most subsites have heavy tails (shape parameters > 0 corresponding to a Frechet [type II] distribution). A minority of sites have shape parameters near zero (Gumbel [type I] distribution with a light tail) or less than zero (Weibull [type III] distribution with a bounded tail).

Although the mean robomussel data depart from a latitudinal cline, GEV analyses reveal latitudinal patterns of environmental variation. The southern sites exhibit warmer conditions on average (in part reflecting water temperatures), indicated by the GEV distribution being centered at higher temperatures (Fig. 4 location parameter). However, the northern sites tend to have fatter tails reflecting a higher incidence of thermal extremes (Fig. 4 shape parameter). The breadth of the temperature distribution does not exhibit a latitudinal cline (Fig. 4 scale parameter). There is considerable variation in GEV parameters within sites corresponding to microclimate variation. GEV distributions—centered at warmer temperatures at the southern sites but possessing a heavier tail at northern sites—produce similar magnitudes of temperatures that are potentially stressful for organisms such as mussels. Consequently, neither the percent of days with temperatures above a 35°C threshold nor the maximum daily temperatures expected to be reached within 100 year intervals (100 year return interval) exhibit pronounced latitudinal patterns (Fig. 4).

Quantitative tools such as Fourier transforms and extreme value statistics are well suited to make sense of complex patterns of environmental variation. Both frameworks can be used to generate future environmental data for incorporation in ecological and evolutionary forecasts (Dillon et al. 2016). Applying

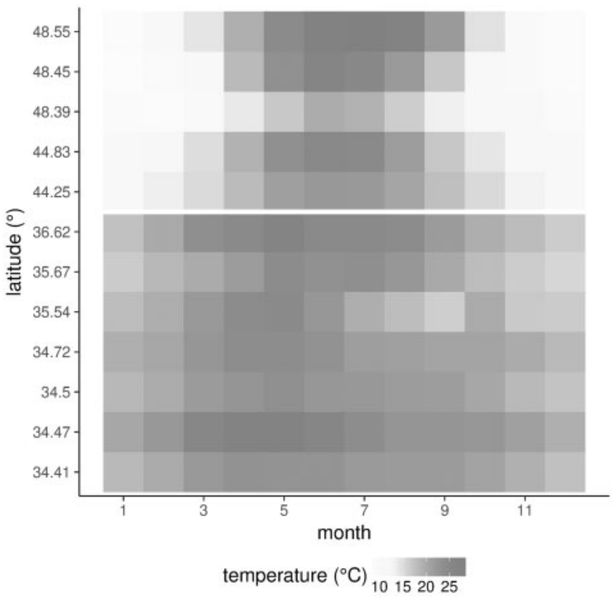


Fig. 3 The mean (across years) of monthly maxima of robomussel daily temperatures departs from smooth latitudinal clines in summer months. Northern sites tend to experience the greatest seasonal fluctuations and the warmest summer extremes. The latitudinal axis is non-linear and the white line delineates northern and southern sites.

the tools highlights the importance of considering spatial variation within sites as well as variation in body temperatures rather than simply environmental temperatures, particularly for sessile organisms such as mussels.

Translating environmental conditions into organismal performance

Laboratory and field measurements of the temperature dependence of organismal performance (e.g., thermal performance curves, TPCs) allow estimating responses to the environment. However, the methodology, conditions, and metrics of physiological and performance measurements often poorly reflect the spatially and temporally variable environments that organisms occupy (Sinclair et al. 2016). We summarize three key pitfalls in applying TPCs to estimate responses to the environment and propose future research needed to address the pitfalls: (1) timescales of measurements are often misaligned with the timescales of organismal response; (2) organismal responses often exhibit threshold temperatures, which are poorly captured in measurements; and (3) organisms respond differentially to temperature across their lifecycle, but measurements are generally restricted to a single life stage (Williams et al. 2016). We additionally advocate for compilations of laboratory and field measurements to facilitate their incorporation in forecasts.

Timescales of responses

Data are increasingly showing that environmental variability and extremes strongly influence organismal responses. For acute thermal stress responses, assessment methods, particularly the rate at which temperature ramps, can bias estimates of critical thermal limits (Terblanche et al. 2007; Rezende et al. 2011). Over longer times scales, growth and development rates vary with whether they are measured at a series of constant temperatures, as is generally done, or in fluctuating temperatures (Kingsolver and Woods 2016). Translating between the timescale of measurement and of organismal responses to environmental variation is an important future objective.

Environmental history also shapes how organisms respond to their environments. The duration, severity, and frequency of past environmental stress determines whether organisms are less sensitive to the stress due to acclimation or more sensitive due to incurred damage or energetic costs (Williams et al. 2016). For example, organisms from variable, stressful environments tend to continuously express heat shock proteins, but have less capacity to induce additional expression in response to an acute thermal stress (Cavicchi et al. 1995; Hofmann and Todgham 2010). Environmental history also influences whether organisms respond to multiple stressors synergistically, additively, or antagonistically (Gunderson et al. 2016). We note that our review focuses on forecasting approaches based on temperature because physiological responses to temperature are better quantified than responses to other environmental conditions. Ignoring other stressors could invalidate forecasts, but we feel it is most tractable for general forecasting approaches to start with forecasting responses to temperature and subsequently build in responses to other, potentially interacting, stressors. Forecasts of responses to multiple stressors for particular organisms will inform future, general forecasts. Resource availability additionally interacts with temperature to determine organismal performance (reviewed by Sinclair et al. 2016).

Thresholds

Organismal responses to environments are generally non-linear and dependent on whether thresholds are crossed. These thresholds include temperatures at which mortality or reproductive failure occurs, activity is limited, or energy or metabolic expenditure

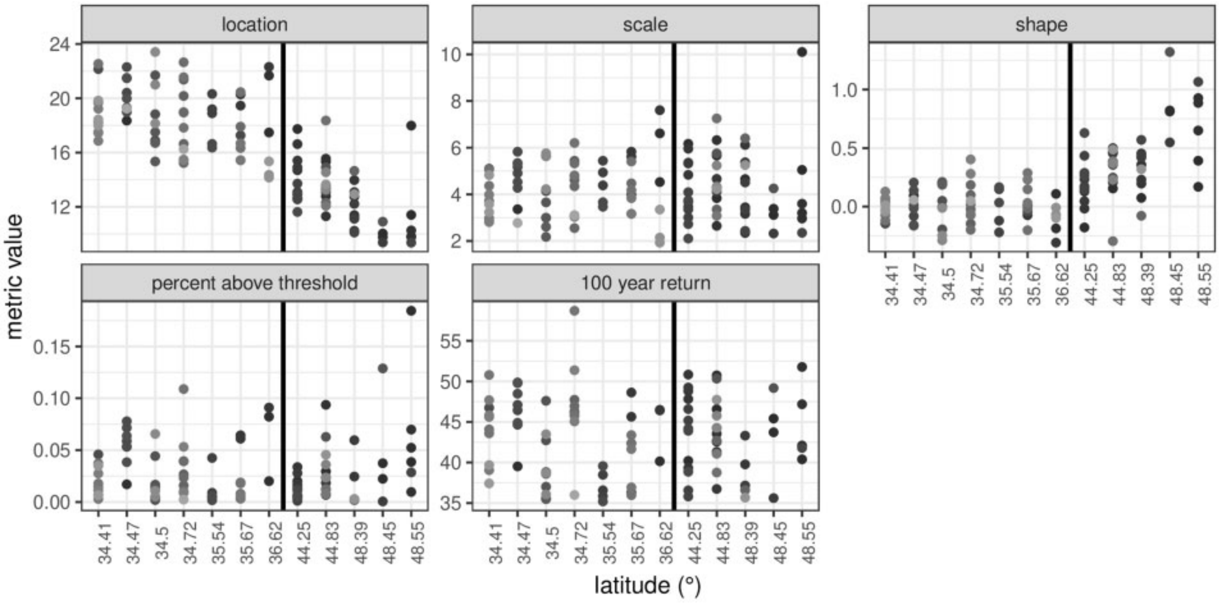


Fig. 4 Generalized extreme value (GEV) statistics provide insight into the likelihood of extreme thermal stress events for intertidal mussels. Within each panel corresponding to a GEV metric, sites are presented along a latitudinal cline on the US West Coast. The vertical line delineates northern and southern sites. The GEV distribution is centered at higher values at southern sites (location parameter) but has a longer tail of extremes at the northern sites (shape parameter). The breadth (scale parameter) is similar across sites. Consequently, the percent of days above a 35°C threshold and the highest temperature estimated to be reached over a 100 year return interval (100 year return) does not exhibit a latitudinal cline.

exceeds supply (Williams et al. 2016). Characterizing thresholds for an organism is a challenge for integrative biologists, particularly because the thresholds are sensitive to timescales of environmental variability and environmental history. For example, dividing a period of cold exposure into shorter, repeated exposures reduced the mortality and also the fitness of flies relative to a single exposure (Marshall and Sinclair 2009). Variation in thresholds also occurs across factors including seasonality, life stage, habitat, and oxygen levels (reviewed by Sinclair et al. 2016).

Integrated consideration of the life cycle

Life stages differ in exposure and sensitivity to their environment (Kingsolver et al. 2011). They vary in microhabitat, coloration, and mobility. Differences can be as dramatic as marine organisms inhabiting pelagic environments as juveniles but intertidal environments as adults (Helmuth et al. 2005). Yet, measurements of thermal sensitivity tend to simplify life cycles or to be restricted to a single life stage (Levy et al. 2015). A comprehensive understanding of the impact of the environment on fitness requires an integrated consideration of environmental exposure and sensitivity across the life cycle that additionally considers environmental seasonality (Williams et al. 2015).

Databases of phenotypes, physiology, and performance measurements

Generalizing to numerous species will require databases compiling physiology and performance measurements. Those measurements that are currently available are often difficult to compare and buried in papers, unpublished theses, and gray literature. Initial traits to include in a database of animals might include critical and lethal thermal limits, preferred body temperatures, physiologically optimum temperatures, and TPCs for key performance measures. Thermal tolerance databases are available (Bennett et al. 2018), but broad databases for animal physiology largely are not (Urban et al. 2016). Morphological and life history data are increasingly available (Jones et al. 2009; Wilman et al. 2014; Myhrvold et al. 2015). Researchers, including those attending a SICB Macrophysiology workshop (http://www.sicb.org/meetings/2013/macrophysiology.php), have called for a comprehensive database for animal phenotypes, physiology, and performance measurements, but progress has been limited.

Databases for animals have lagged behind those for plants (Kattge et al. 2011) in part because plant ecologists and physiologists have agreed upon standard measurements and measurement techniques (Cornelissen et al. 2003). Agreement on protocols was eased by most plants having an important and restricted unit of focus (leaves) and appropriate and widely available tools (e.g., Licor 6400 photosynthesis system) to quantify relevant traits. Although consensus protocols may be more elusive for animals, they are essential. A recent paper compiles protocols for functionally-relevant traits of terrestrial invertebrates (Moretti et al. 2017) and may provide an initial step toward a comprehensive database. Machine learning initiatives (e.g., the opensource *DeepDive* and *Snorkel* initiatives) designed to extract data from publications have succeeded in constructing paleontology databases and may aid construction of an animal phenotype database (Peters et al. 2014). However, vetting and hand curating are often required to extract data from unstructured content.

The Global Biotraits Database (Dell et al. 2013) primarily compiles the thermal responses of ecological rather than physiological traits, but it illustrates the database challenges. Measurements tend to span a restricted range of temperatures relative to those organisms experience and to omit stressful or extreme temperatures (Fig. 5a). Measurements are often taken at a low number of constant temperatures (Fig. 5b), which makes it challenging to understand responses to variable environments (Kingsolver and Woods 2016; Williams et al. 2016). These characteristics reduce accuracy and often lead to extrapolation when describing thermal responses.

Ecological and evolutionary consequences of climate change

A particularly challenging component of forecasts is estimating fitness components from performance. Environmental variation and subsequent performance variation makes the estimation especially challenging (Martin and Huey 2008; Vasseur et al. 2014; Denny 2017). A viable approach is to translate performance into fecundity via the currencies of energy or time (Dunham 1993). Periods of low performance or conditions that preclude performance may reduce survival. One problem with fitness estimates is that most modeling is based on assuming linear (proportional and unidirectional) responses to mean environmental conditions. Yet, almost all organismal responses are non-linear and variable over short time periods.

As environmental and biological data increase in availability, techniques for temporal aggregation that reflect how organisms integrate climatic histories over their lives are needed (Huey et al. 2012). The sequence of environmental conditions, particularly time for recovery, determines the incidence of thermal stress. An appropriate aggregation would reflect non-linearities in biological responses (such as rapidly increasing biological rates with increasing temperatures) and thresholds (such as temperature cutoffs for activity). Translating environmental conditions into metrics such as body temperatures, performance, or energetics at temporal intervals matching that of biological responses enables appropriate aggregation. These aggregation approaches would complement many ecological forecasting models, such as ENMs that are generally based on mean environmental conditions (Buckley et al. 2010).

Forecasting approaches that estimate fitness associated with phenotypes can be used to predict evolution. They allow estimating selection as well as considering the fitness consequences of acclimation and plasticity (defined to include all forms of phenotypic change, from long-term irreversible to short-term reversible). The interplay of plasticity and selection will be central to responses to climate change. Plasticity can slow evolution by buffering selection. For example, behavioral thermoregulation by lizards can initially buffer thermal stress associated with climate change, but can ultimately confer sensitivity to climate change by reducing selection (Huey et al. 2012; Buckley et al. 2015). Conversely, plasticity can facilitate evolution by enabling persistence or reducing variability in the direction and magnitude of selection associated with environmental variability (Chevin et al. 2010; Hendry 2015). Linking phenotypes to fitness suggests that the latter is the case for *Colias* butterflies: phenotypic plasticity can reduce variation in selection in response to both seasonality and interannual temperature variability and ultimately facilitate evolution in response to climate warming (Kingsolver and Buckley 2017).

Much additional research is needed to develop robust and general approaches to estimating fitness based on information about phenotypes and environments. For example, field experiments assessing selection in variable natural environments are needed to confirm predicted linkages between phenotypes, performance, and fitness. Emerging "omic" approaches (such as using genomics to infer the genetic basis of adaptation, using epigenetics to assess plasticity, and using metabolomics to assess the energetic implications of environments) offer promise in uncovering the genetic basic of responses to the environment as well as plasticity and selection in response to environmental variability and change (Bay et al. 2017). This information from omics will enable forecasts to better translate from environmental conditions to performance to fitness and evolution. Omic approaches will be particularly valuable

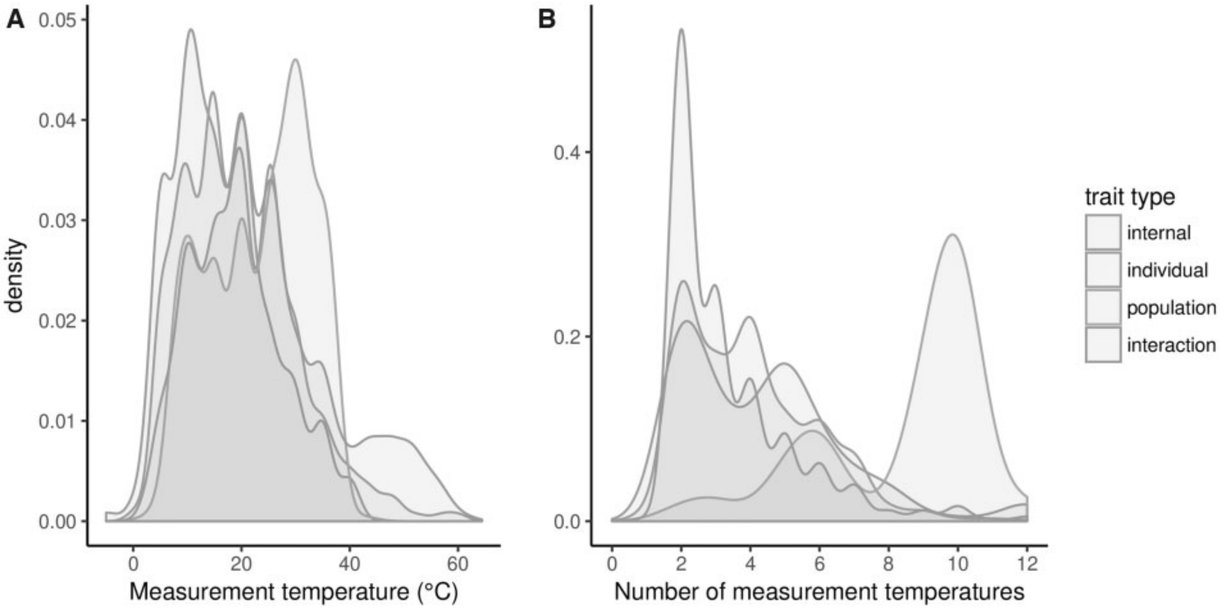


Fig. 5 The Global Biotraits Database (Dell et al. 2013) illustrates limitations in thermal response measurements. Measurements tend to be (**A**) focused on a restricted range of temperatures relative to those that organisms experience and (**B**) include a low number of constant temperatures. Traits are divided according whether they are internal (internal to the organism); individual (at the level of individual organisms that include mechanical interactions with the external environment); population (processes for a group of conspecific individuals); or interaction (involving interaction between two or more species).

for ecological forecasting when coupled with controlled laboratory or field environmental manipulations, common gardens, or reciprocal transplants (Hoffmann and Sgrò 2011). Many evolutionary forecasts will likely need to rely on quantitative genetic models because many traits involved in temperature dependence are determined by complex genetic mechanisms (Reusch and Wood 2007; Gienapp et al. 2008; Shaw and Etterson 2012). Finally, experiments are needed to assess heritability of such traits for use in evolutionary forecasts.

Models translating from environmental conditions and phenotypes to performance and ultimately fitness may be considered null models for forecasting. Other factors including species interactions and dispersal limitations that we omit here may strongly impact fitness and population dynamics and should subsequently be incorporated (Buckley et al. 2010; Urban et al. 2016). Although we have focused on estimating fitness from performance, the approach is complementary to other approaches being developed (Dietze 2017).

Forecasting challenges

Progress toward meeting these challenges has been occurring steadily since previous reviews (e.g., Helmuth et al. 2005; Kearney and Porter 2009; Buckley et al. 2010; Huey et al. 2012), but many challenges persist (Sinclair et al. 2016; Urban et al. 2016; Dietze et al. 2018). Improving our capacity for ecological and evolutionary forecasting depends on adequately characterizing organismal responses to spatially and temporally variable environments. Physiological, performance, and fitness responses to environmental fluctuations and extremes are characterized by nonlinearities and thresholds. Responses and whether they are modified by stress, acclimation, or plasticity are contingent on the environmental histories organisms have experienced. Environmental sensitivities vary across organisms' lifecycles. Microclimate selection and other forms of behavioral buffering alter how organisms experience environmental fluctuations. Accounting for all these complications of organism–environment interactions can be daunting, but emerging data and models promise to improve forecasts (Urban et al. 2016).

Much progress toward meeting these challenges has come in the form of delving into the empirical details of how the environment influences organismal performance and fitness and building forecasting approaches for particular organisms. The accumulation of these studies has positioned the research community to meet the challenges by generalizing understanding and approaches. Meeting the challenges is likewise aided by nearly 10 years of effort toward meeting the SICB grand challenges in organismal biology (Schwenk et al. 2009).

Over the next decade, we hope to see substantial progress toward solving the following challenges:

1. Sensing the environment at scales relevant to organismal physiology:
    a. We need low-cost dataloggers with probes capable of collecting data on multiple environmental variables at scales appropriate to organisms. This goal will be facilitated by developing simple manuals and knowledge sharing initiatives for building data loggers from low-cost, simple-to-use microcontrollers and other technologies.
    b. We require descriptions of spatial microclimates that can be obtained by environmental sensing technology including drones and satellites. Citizen science projects and private initiatives (e.g., www.planet.com) have the potential to rapidly augment data availability and enhance data accuracy and spatiotemporal resolution.
    c. We need microclimate and biophysical models capable of integrating data to accurately predict the body temperatures and conditions of organisms in their microclimates. The NicheMapR package is increasing awareness and usability of these tools but we encourage the release of source code to increase transparency. We invite anyone interested to contribute to our open-source initiative (trenchproject.github.io) or others.

Assessment: Emerging technologies and a push toward open computing should enable meeting this challenge within the decade.

2. Translating environmental conditions into organismal performance:
    a. We need more and better biological data if our forecasts are to improve. We hope to see the development of a database compiling animal phenotypic, physiological, and performance measurements relevant to forecasting. Design of the database should be done by consensus of a group willing to struggle with the methodological issues outlined above. What methodologies will be tractable while retaining the essential details of organisms' non-linear responses to their environments? Are there standard kinds of microclimatic, physiological, and environmental data that should be collected? Large scale initiatives to collect data for numerous species in a systematic manner will be required to fill and maintain the database (Urban et al. 2016).

Assessment: We see the development of databases, particularly those containing phenotypes, as the most urgent forecasting challenge, which we hope funders will help meet.

3. Ecological and evolutionary consequences of climate change:
    a. Publishing well-documented code (Mislan et al. 2016), release of software packages, and ideally developing common standards for model parameterization and data formats (e.g., Zoon R package, github.com/zoonproject/zoon) will speed modeling progress. Models and data collection efforts need to proceed in concert.
    b. Although forecasting techniques are proliferating, many remain poorly tested (Maguire et al. 2015). Historical data, including environmental data, phenotypes, and ecological survey data, are necessary to test models. Necessary ecological data include phenology, distribution, and abundance data. Focusing on a select but diverse set of organisms (e.g., initially several ectothermic [insect and lizard] species, but eventually endotherms) would aid tractability. We need to assemble and disseminate both recent and paleo datasets for testing models. Historical data for model testing are currently limited, but we must collect data in a manner such that it can be used for future model testing.
    c. The development of forecasting approaches should be forward-thinking and harness the potential of new types of data (e.g., omics) that may be readily available in the near future.

Assessment: General forecasting models are likely a distant reality, but practicing open-source science aimed at increasing reproducibility (Parker et al. 2016) and prioritizing model testing and adaptability will accelerate progress.

These and other challenges have led to continued predominance of statistical forecasting techniques that ignore important aspects of organism–environment interactions and perform poorly at predicting responses to past environmental changes (Maguire et al. 2015). Forecasting approaches that better account for temporal and spatial environmental variation and its influence on organismal physiology, performance, and fitness are overdue. Despite the difficulty, it is time to dedicate substantial effort and resources to improving forecasting models and collecting necessary data for parameterization. We need to accelerate the search for a middle ground to forecasting-models that are sufficiently simple to be generalized to numerous species but that include the complexities of how organisms respond to their temporally and spatially variable environments necessary for robust forecasts. And we need the help of diverse organismal biologists from within SICB and beyond.

Acknowledgments

We thank the ICB editors for the opportunity to contribute a perspective. Thanks in particular to Art Woods for extensive suggestions. Thanks to Brian Helmuth, Ray Huey, Michael Kearney, Sylvain Pincebourde, Janneke HilleRisLambers and members of her laboratory, and an anonymous reviewer for comments that greatly improved the manuscript.

Funding

This work was supported by the National Science Foundation [DBI-1349865 to L.B.B. and IGERT DGE-1258485 fellowship to A.F.C.].

References

Allan BM, Ierodiaconou D, Nimmo DG, Herbert M, Ritchie EG. 2015. Free as a drone: ecologists can add UAVs to their toolbox. Front Ecol Environ 13:354–5.

Anderson K, Gaston KJ. 2013. Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Front Ecol Environ 11:138–46.

Angilletta MJ Jr, Sears MW. 2011. Coordinating theoretical and empirical efforts to understand the linkages between organisms and environments. Integr Comp Biol 51:653–61.

Bakken GS. 1992. Measurement and application of operative and standard operative temperatures in ecology. Integr Comp Biol 32:194–216.

Barnard HR, Findley MC, Csavina J. 2014. PARduino: a simple and inexpensive device for logging photosynthetically active radiation. Tree Physiol 34:640–5.

Bay RA, Rose N, Barrett R, Bernatchez L, Ghalambor CK, Lasky JR, Brem RB, Palumbi SR, Ralph P. 2017. Predicting responses to contemporary environmental change using evolutionary response architectures. Am Nat 189:463–73.

Bennett JM, Calosi P, Clusella-Trullas S, Martínez B, Sunday J, Algar AC, Araújo MB, Hawkins BA, Keith S, Kühn I, et al. 2018. GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. Sci Data 5:180022.

Boyle SA, Kennedy CM, Torres J, Colman K, Pérez-Estigarribia PE, de la Sancha NU. 2014. High-resolution satellite imagery is an important yet underutilized resource in conservation biology. PLoS One 9:e86908.

Bramer I, Anderson BJ, Bennie J, Bladon AJ, De Frenne P, Hemming D, Hill RA, Kearney MR, Körner C, Korstjens AH, et al. 2018. Advances in monitoring and modelling climate at ecologically relevant scales. Adv Ecol Res 58:101–61.

Buckley LB, Ehrenberger JC, Angilletta MJ. 2015. Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. Funct Ecol 29:1038–47.

Buckley LB, Kingsolver JG. 2012. Functional and phylogenetic approaches to forecasting the ecological impacts of climate change. Annu Rev Ecol Evol Syst 43:205–26.

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW. 2010. Can mechanism inform species' distribution models? Ecol Lett 13:1041–54.

Campbell G, Norman J. 2000. An introduction to environmental biophysics. New York (NY): Springer.

Cavicchi S, Guerra D, Torre VL, Huey RB. 1995. Chromosomal analysis of heat-shock tolerance in *Drosophila melanogaster* evolving at different temperatures in the laboratory. Evolution 49:676–84.

Chevin LM, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biol 8:e1000357.

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Steege H. Ter Morgan H, Van Der Heijden MGA, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335–80.

Dell AI, Pawar S, Savage VM. 2013. The thermal dependence of biological traits. Ecology 94:1205–6.

Denny M. 2017. The fallacy of the average: on the ubiquity, utility and continuing novelty of Jensen's inequality. J Exp Biol 220:139–46.

Denny M, Helmuth B. 2009. Confronting the physiological bottleneck: a challenge from ecomechanics. Integr Comp Biol 49:197–201.

Denny MW, Gaines S. 2002. Chance in biology: using probability to explore nature. Princeton (NJ): Princeton University Press.

Denny MW, Hunt LJH, Miller LP, Harley CDG. 2009. On the prediction of extreme ecological events. Ecol Monogr 79:397–421.

Dietze MC. 2017. Ecological forecasting. Princeton (NJ): Princeton University Press.

Dietze MC, Fox A, Beck-Johnson LM, Betancourt JL, Hooten MB, Jarnevich CS, Keitt TH, Kenney MA, Laney CM, Larsen LG, et al. 2018. Iterative near-term ecological forecasting: needs, opportunities, and challenges. Proc Natl Acad Sci U S A 115:1424–32.

Dillon ME, Woods HA. 2016. Introduction to the symposium: beyond the mean: biological impacts of changing patterns of temperature variation. Integr Comp Biol 56:11–3.

Dillon ME, Woods HA, Wang G, Fey SB, Vasseur DA, Telemeco RS, Marshall K, Pincebourde S. 2016. Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. Integr Comp Biol 56:14–30.

Dunham AE. 1993. Population responses to environmental change: physiologically structured models, operative environments, and population dynamics. In: Kareiva PM, Kingsolver JG, Huey RB, editors. Biotic interactions and global change. Sunderland (MA): Sinauer. p. 95–119.

Dzialowski EM. 2005. Use of operative temperature and standard operative temperature models in thermal biology. J Therm Biol 30:317–34.

Faye E, Dangles O, Pincebourde S. 2016. Distance makes the difference in thermography for ecological studies. J Therm Biol 56:1–9.

Faye E, Rebaudo F, Yánez-Cajo D, Cauvy-Fraunié S, Dangles O. 2016. A toolbox for studying thermal heterogeneity across spatial scales: from unmanned aerial vehicle imagery to landscape metrics. Methods Ecol Evol 7:437–46.

Gates DM. 1980. Biophysical ecology. New York (NY): Springer-Verlag.

Gienapp P, Teplitsky C, Alho JS, Mills JA, Merilä J. 2008. Climate change and evolution: disentangling environmental and genetic responses. Mol Ecol 17:167–78.

Gilman SE, Wethey DS, Helmuth B. 2006. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. Proc Natl Acad Sci U S A 103:9560–5.

Gunderson AR, Armstrong EJ, Stillman JH. 2016. Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. Annu Rev Mar Sci 8:357–78.

Helmuth B. 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. Integr Comp Biol 42:837–45.

Helmuth B, Broitman BR, Yamane L, Gilman SE, Mach K, Mislan KAS, Denny MW. 2010. Organismal climatology: analyzing environmental variability at scales relevant to physiological stress. J Exp Biol 213:995–1003.

Helmuth B, Choi F, Matzelle A, Torossian JL, Morello SL, Mislan KAS, Yamane L, Strickland D, Szathmary PL, Gilman SE, et al. 2016. Long-term, high frequency in situ measurements of intertidal mussel bed temperatures using biomimetic sensors. Sci Data 3:160087.

Helmuth B, Kingsolver JG, Carrington E. 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? Annu Rev Physiol 67:177–201.

Hendry AP. 2015. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. J Hered 107:25–41.

Hoffmann AA, Sgrò CM. 2011. Climate change and evolutionary adaptation. Nature 470:479–85.

Hofmann GE, Todgham AE. 2010. Living in the now: physiological mechanisms to tolerate a rapidly changing environment. Annu Rev Physiol 72:127–45.

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos Trans R Soc B Biol Sci 367:1665–79.

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648.

Kaspari M, Clay NA, Lucas J, Yanoviak SP, Kay A. 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Glob Change Biol 21:1092–102.

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, et al. 2011. TRY—a global database of plant traits. Glob Change Biol 17:2905–35.

Kays R, Crofoot MC, Jetz W, Wikelski M. 2015. Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

Kearney M, Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol Lett 12:334–50.

Kearney MR, Isaac AP, Porter WP. 2014. Microclim: global estimates of hourly microclimate based on long-term monthly climate averages. Sci Data 1:140006.

Kearney MR, Porter WP. 2017. NicheMapR—an R package for biophysical modelling: the microclimate model. Ecography 40:664–74.

Kearney MR, Shamakhy A, Tingley R, Karoly DJ, Hoffmann AA, Briggs PR, Porter WP. 2014. Microclimate modelling at macro scales: a test of a general microclimate model integrated with gridded continental-scale soil and weather data. Methods Ecol Evol 5:273–86.

Kingsolver JG, Buckley LB. 2017. Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. Phil Trans R Soc B 372:20160147.

Kingsolver JG, Woods HA. 2016. Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. Am Nat 187:283–94.

Kingsolver JG, Woods HA, Buckley LB, Potter KA, MacLean HJ, Higgins JK. 2011. Complex life cycles and the responses of insects to climate change. Integr Comp Biol 51:719–32.

Levy O, Buckley LB, Keitt TH, Smith CD, Boateng KO, Kumar DS, Angilletta MJ. 2015. Resolving the life cycle alters expected impacts of climate change. Proc R Soc B Biol Sci 282:20150837.

Levy O, Buckley LB, Keitt TH, Angilletta MJ. 2016. A dynamically downscaled projection of past and future microclimates. Ecology 97:1888.

Lockridge G, Dzwonkowski B, Nelson R, Powers S. 2016. Development of a low-cost arduino-based sonde for coastal applications. Sensors 16:528.

MacLean SA, Beissinger SR. 2017. Species' traits as predictors of range shifts under contemporary climate change: a review and meta-analysis. Glob Change Biol 23:4094–105.

Maguire KC, Nieto-Lugilde D, Fitzpatrick MC, Williams JW, Blois JL. 2015. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. Annu Rev Ecol Evol Syst 46:343–68.

Marshall KE, Sinclair BJ. 2009. Repeated stress exposure results in a survival–reproduction trade-off in *Drosophila melanogaster*. Proc R Soc Lond B Biol Sci 277:963–9.

Martin TL, Huey RB. 2008. Why suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. Am Nat 171:E102–18.

Mislan KAS, Heer JM, White EP. 2016. Elevating the status of code in ecology. Trends Ecol Evol 31:4–7.

Moretti M, Dias ATC, de Bello F, Altermatt F, Chown SL, Azcárate FM, Bell JR, Fournier B, Hedde M, Hortal J, et al. 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Funct Ecol 31:558–67.

Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology 96:3109.

Mykles DL, Ghalambor CK, Stillman JH, Tomanek L. 2010. Grand challenges in comparative physiology: integration across disciplines and across levels of biological organization. Integr Comp Biol 50:6–16.

Nadeau CP, Urban MC, Bridle JR. 2017. Coarse climate change projections for species living in a fine-scaled world. Glob Change Biol 23:12–24.

Norris JR, Allen RJ, Evan AT, Zelinka MD, O'Dell CW, Klein SA. 2016. Evidence for climate change in the satellite cloud record. Nature 536:72–5.

Parker TH, Forstmeier W, Koricheva J, Fidler F, Hadfield JD, Chee YE, Kelly CD, Gurevitch J, Nakagawa S. 2016. Transparency in ecology and evolution: real problems, real solutions. Trends Ecol Evol 31:711–9.

Peters SE, Zhang C, Livny M, Ré C. 2014. A machine-compiled macroevolutionary history of Phanerozoic life. ArXiv Prepr ArXiv14062963.

Porter WP, Gates DM. 1969. Thermodynamic equilibria of animals with environment. Ecol Monogr 39:227–44.

Porter WP, Mitchell JW, Beckman WA, DeWitt CB. 1973. Behavioral implications of mechanistic ecology. Oecologia 13:1–54.

Porter WP, Tracy CR. 1983. Biophysical analyses of energetics, time-space utilization, and distributional limits. Cambridge (MA): Harvard University Press.

Potter KA, Woods HA, Pincebourde S. 2013. Microclimatic challenges in global change biology. Glob Change Biol 19:2932–9.

Reusch TBH, Wood TE. 2007. Molecular ecology of global change. Mol Ecol 16:3973–92.

Rezende EL, Tejedo M, Santos M. 2011. Estimating the adaptive potential of critical thermal limits: methodological problems and evolutionary implications. Funct Ecol 25:111–121.

Scheffers BR, De Meester L, Bridge TC, Hoffmann AA, Pandolfi JM, Corlett RT, Butchart SH, Pearce-Kelly P, Kovacs KM, Dudgeon D, et al. 2016. The broad footprint of climate change from genes to biomes to people. Science 354:aaf7671.

Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA. 2014. Microhabitats reduce animal's exposure to climate extremes. Glob Change Biol 20:495–503.

Schwenk K, Padilla DK, Bakken GS, Full RJ. 2009. Grand challenges in organismal biology. Integr Comp Biol 49:7–14.

Sears MW, Angilletta MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA. 2016. Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. Proc Natl Acad Sci U S A 113:10595–600.

Shaw RG, Etterson JR. 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. New Phytol 195:752–65.

Sih A, Stamps J, Yang LH, McElreath R, Ramenofsky M. 2010. Behavior as a key component of integrative biology in a human-altered world. Integr Comp Biol 50:934–44.

Sinclair BJ, Marshall KE, Sewell MA, Levesque DL, Willett CS, Slotsbo S, Dong Y, Harley CDG, Marshall DJ, Helmuth BS, et al. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecol Lett 19:1372–85.

Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc Natl Acad Sci U S A 111:5610–5.

Sutton JR, Lakshmi V. 2017. From space to the rocky intertidal: using NASA MODIS sea surface temperature and NOAA water temperature to predict intertidal logger temperature. Remote Sens 9:162.

Terblanche JS, Deere JA, Clusella-Trullas S, Janion C, Chown SL. 2007. Critical thermal limits depend on methodological context. Proc R Soc B Biol Sci 274:2935–43.

Turner W, Rondinini C, Pettorelli N, Mora B, Leidner AK, Szantoi Z, Buchanan G, Dech S, Dwyer J, Herold M, et al. 2015. Free and open-access satellite data are key to biodiversity conservation. Biol Conserv 182:173–6.

Urban MC, Bocedi G, Hendry AP, Mihoub JB, Pe'er G, Singer A, Bridle JR, Crozier LG, De Meester L, Godsoe W, et al. 2016. Improving the forecast for biodiversity under climate change. Science 353:aad8466.

Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CDG, McCann KS, Savage V, Tunney TD, O'Connor MI. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proc R Soc B Biol Sci 281:20132612.

Veloz SD, Williams JW, Blois JL, He F, Otto-Bliesner B, Liu Z. 2012. No-analog climates and shifting realized niches during the late Quaternary: implications for 21st-century predictions by species distribution models. Glob Change Biol 18:1698–713.

Wang G, Dillon ME. 2014. Recent geographic convergence in diurnal and annual temperature cycling flattens global thermal profiles. Nat Clim Chang 4:988.

Williams CM, Buckley LB, Sheldon KS, Vickers M, Pörtner H-O, Dowd WW, Gunderson AR, Marshall KE, Stillman JH. 2016. Biological impacts of thermal extremes: mechanisms and costs of functional responses matter. Integr Comp Biol 56:73–84.

Williams CM, Henry HA, Sinclair BJ. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biol Rev 90:214–35.

Williams JW, Kharouba HM, Veloz S, Vellend M, McLachlan J, Liu Z, Otto-Bliesner B, He F. 2013. The ice age ecologist: testing methods for reserve prioritization during the last global warming. Glob Ecol Biogeogr 22:289–301.

Wilman H, Belmaker J, Simpson J, de la Rosa C, Rivadeneira MM, Jetz W. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. Ecology 95:2027.

Woods HA, Dillon ME, Pincebourde S. 2015. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. J Therm Biol 54:86–97.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 52–57
doi:10.1093/icb/icy034

Society for Integrative and Comparative Biology

SYMPOSIUM INTRODUCTION

Science in the Public Eye: Leveraging Partnerships—An Introduction

Martha Merson,[1,*] Louise C. Allen[†] and Nickolay I. Hristov[‡]

*TERC, Cambridge, MA, USA; †Winston-Salem State University, Winston-Salem, NC, USA; ‡Center for Design Innovation, 450 Design Ave, Winston-Salem, NC 27101, USA

From the symposium "Science in the Public Eye: Leveraging Partnerships" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1] E-mail: martha_merson@terc.edu

Synopsis With stories of struggle and dramatic breakthroughs, science has incredible potential to interest the public. However, as the rhetoric of outrage surrounds controversies over science policy there is an urgent need for credible, trusted voices that frame science issues in a way that resonates with a diverse public. A network of informal educators, park rangers, museum docents and designers, and zoo and aquarium interpreters are prepared to do so during millions of visits a year; just where science stories are most meaningfully told—in the places where members of the public are open to learning. Scientific researchers can benefit from partnerships with these intermediaries who are accorded status for their trustworthiness and good will, who have expertise in translating the science using language, metaphors, encounters, and experiences that are appropriate for non-experts. In this volume, we describe and probe examples wherein scientists work productively with informal educators and designers, artists, staff of federal agencies, citizen scientists, and volunteers who bring science into the public eye.

Introduction

In so many ways today's science communication is not our parents' experience of science communication. Authoritative male voices dominated the soundscape during the 20th century. Communication strategies channeled the flow of science information from expert to public. Experts assumed that a better informed public would value scientific research and make scientifically informed decisions (Irwin and Wynne 1996). In shifting to a science communication model that prioritizes public engagement, individuals' interests, questions, and motivations become central (McCallie et al. 2009; Storksdieck et al. 2016). The National Resource Council consensus report (2009) highlights the role that informal science learning institutions like zoos, science centers, and parks play in fostering engagement. A wide variety of settings makes it possible for the public to encounter science and scientists themselves in different ways, some more visual, playful, and explicitly instructive than others (National Research Council 2009; Storksdieck et al. 2016).

Funders expect scientists to engage with audiences beyond their peers and colleagues as Alpert and Risien and Storksdieck point out in their articles in this volume. Clearly when scientists leave university lecture halls for science cafes, museums, and community science fairs, opportunities for bi-directional dialog increase. To prepare scientists for speaking in these settings, the Alda Center for Communicating Science at Stonybrook University uses improvisational games to enhance connections between presenters and public audiences. The Story Collider team offers coaching on personal science stories, while Portal to the Public, a collaboration funded by the National Science Foundation, initiated a robust model for museums to structure and sustain opportunities for scientists to engage the public in their current research (Selvakumar and Storksdieck 2013). Nowadays conversations between the public and scientists about their experiences as learners, as research assistants, and investigators frequently occur in science centers, and emerging scientists are eager to engage in these conversations (Storksdieck et al. 2017).

Setting expectations for scientists to communicate with the public does little to solve the dilemma scientists face: how to fit public appearances in among their research, teaching, and obligations to their institutions. Wildlife biologists and long-time SICB members Hristov and Allen teamed up with informal education researcher, Merson, from TERC in 2013. TERC's expertise in STEM learning and teaching infused the new team's scientific outreach efforts in national parks with inquiry approaches. After participating in professional development, park rangers began engaging park visitors in conversations about the methods and relevance of the research (see Allen et al. this volume). Based on the enthusiastic response to the joint effort, Interpreters and Scientists Working on Our Parks (iSWOOP), we proposed the symposium, Science in the Public Eye: Leveraging Partnerships. We stepped into this arena, determined to showcase projects and models that do not require scientists to shoulder the responsibility for public engagement alone. We recruited presenters who could speak to the challenges and opportunities of partnerships. We encouraged examples and practical recommendations for how scientists could go about leveraging opportunities. Throughout the symposium and in the papers in this volume, presenters set out to inspire emerging and established scientists and researchers alike to think strategically about the sort of partnerships they could initiate or benefit from to achieve broader impacts so that perfecting their ability to communicate about science and then communicating science don't eclipse doing science.

We, iSWOOP's project leaders, promote partnerships between those scientists who have limited capacity to devote to outreach and public engagement and professionals whose job it is to engage the public in science in out-of-school settings. The approach has proven successful and popular. When education rangers in national parks who have the jobs most closely akin to museum docents and science center floor staff, hear about iSWOOP, they nod. They speak eloquently to the need for access to published current, park-based, park-relevant science, and the scientists themselves (see the first video on offer here: http://www.iswoopparks.com/about/project-description/, for example). Opportunities for interpreters to hear firsthand about scientific studies, give accounts of phenomena from their place-based observations, and exchange stories and questions with scientists are welcome, but relatively rare (MacDonald 2013; Char 2015; Merson et al. 2017). Once iSWOOP brings together scientists, park rangers and informal science educators for classroom-based and field-based professional development (see Allen et al. this volume), more visitors begin to see and hear about the many park-based and park-relevant science projects that happen behind the scenes. Trusted by the public, dedicated to science translation, and skilled at crafting stories for multi-age audiences, park rangers are ideal ambassadors for the science that too often gets left out of the public discourse. This is the message we wanted to bring to members of the Society for Integrative and Comparative Biology: dedicated and talented partners await you in a venue that makes sense for your science.

More than the facts

Science is more than anything the pursuit of questions, figuring out ways to find out what we don't know. It is about revising the record, constantly refining what we know. It is about how we know and not taking on faith, but being intrigued with new ways to investigate our world. It is about using science for us, our lives, our comfort, and our decisions. While we rely on science to explain how the world works, these less traditionally visible aspects of science scholarship are worth valuing and promoting in informal settings. In the educational literature, they are science process standards and they are integral to inquiry (National Academy of Sciences 1995). The symposium organizers, iSWOOP project leaders and advisors, have distilled these four belief statements to counteract the sticky notion that science is about factual information gathered by white men working alone in windowless labs. We owe a debt to Stuart Firestein (2012) for his formulation of the role of questions in scientific research.

- Science is about questions, finding, and exploring the next question.
- Scientific research is full of compelling stories of how we know what we know.
- Science is about constant revision; the facts will change.
- Science matters when we, collectively, use it to inform decisions.

Contributors to the recent *Legacy Magazine* issue on science communication issued by the National Association for Interpretation concur with the need to dwell on the idea of science as constant revision. Holt (2017) writes:

> We want to operate on that brink, challenging audiences to think critically and become involved by realizing that the scientific process is on-going.

> To do this, we must take up the information where the scientists left off by remembering what science is at its fundamental core: questioning everything. . . . One new finding can completely change the story we thought we were telling. . . .

By introducing the reality that what people are learning today could be refuted in the future, interpreters free their audiences from a sense that everything in the world is understood.

Credible voices needed

Turning over one's science for others to translate can be nerve-wracking. University-based scientists rightly perceive that speaking about implications of their research outside of professional circles carries risks to their credibility with consequences—from perceived advocacy, overstated claims, or imprecise statements (often made by the media on their behalf) (Horton et al. 2016). Credibility is easily lost. Misrepresentation can have fearsome consequences (see Elin Roberts, The Bacon Sandwich, for example, https://www.storycollider.org/stories/2016/1/1/elin-roberts-the-bacon-sandwich).

In this introduction, we lay out the potential for partnerships to increase the delivery and visibility of science through trusted channels. Widespread skepticism based on perceptions of corporation-slanted (funded) research, and media and government more generally, make partnerships with trusted institutions valuable and critical (Nisbet 2014). Such institutions and their staff members, particularly the intermediaries in the world of informal, out-of-school learning, can make scientific research visible and place members of the public closer to the science process (National Research Council 2009).

Interpreters and scientists face quite different challenges in communicating to the public about scientific research. Among their peers, scientists' credibility is tied to precision. Their training leads them to highlight details, facts, and to hedge (Olson 2009). They fear their credibility will suffer if they overstate claims or are perceived as advocates for policies rather than neutral fact-givers (Jensen 2008; Horton et al. 2016). Intermediaries are regarded as knowledgeable if they work in an exhibit or park. Some have doctorates and accumulated expertise, but many are generalists, hired for their ability to communicate. Their credibility derives from their goodwill toward the public and perceptions of their trustworthiness (Fig. 1). In organizational literature, trustworthiness includes benevolence as well as ability and integrity. Mayer et al. (1995) argue that ability, benevolence, and integrity are important to trust, and each may vary independently of the others.

Similar to firefighters, park rangers epitomize trustworthiness as their actions are predicated on concern for others' safety and well-being. Looking at the criteria Mayer et al. (1995) set out for achieving trust, park rangers, like museum docents, and other intermediaries have little motivation to lie. They don't benefit financially from their interactions with the public. They do not get ahead by misrepresenting research. Their mission is to reveal the significance of natural and cultural resources, to arouse wonder and awe (Ham 2013). Whereas scientists have an allegiance to data, to their subject, or discipline, interpreters' stature and success are inextricably linked to visitors' experience. If visitors are satisfied, comment positively, and return for more, the interpreters are successful.

Transparency is critical to trust. When science is physically removed from many people's view and daily life, a breach in transparency results. Perceptions of legitimate, transparent, and/or binding procedures enable confidence in others (Stern and Coleman 2015). Partnerships that give the science process visibility, such as the projects described in this volume, restore transparency and thereby contribute to the perception that science is a collective endeavor, a human enterprise with human stories of success and failure, creativity, and dogged determination. The contributing authors are active and visible in their fields. In more than one case, their contributions are synthesized slices of decades of work. But this compendium is a first for them to be published in each other's company, visible to the community of organismal biologists. This is another aspect of transparency that is relevant to leveraging partnerships.

Possible venues, allies, and outcomes

In this volume, authors testify that new partnerships require an investment of time and energy and determination. Unfortunately, scientists, journalists, and educators concerned about research and learning do not have the luxury of putting them off for another day; basic research is under attack now (Zimmer 2018). As scientists seek new partners for outreach and education, all of the authors recommend explicitly discussing expectations (e.g., Alpert; King et al. this volume; as well as Gill et al. this volume and Harrower et al., this volume). Naming the expected outcomes, audience, funding sources, and time commitments keeps everyone's expectations realistic.

Fig. 1 Scientists and interpreters derive credibility in different ways.

In this volume, we learn from those who have worked productively with environmental educators, designers, and others who can give visibility to the scientists' research. The world of informal learning is extensive and varied, lifelong, and life-wide (Sacco et al. 2014). Researchers of informal education impacts are looking at the diversity of out-of-school learning as its own ecology (Bevan 2016). Therefore, we recommend that readers approach the articles by thinking about the venue and the allies being described, that is the intermediaries who are well-positioned to assist in bringing science into the public eye. In each venue, scientists will invest effort. What that investment looks like will vary from fund-raising to participating in professional development to sharing protocols. The possible outcomes on the public are equally varied (Besley et al. 2015) (see Table 1). Julie Risien and Martin Storksdieck's article opens this issue, framing the importance of delineating an individual impact identity that takes into account variations in scientists' individuals' strengths, their institutional context, the nature of their research, and the desired outcomes of their public engagement activities. The authors argue that a more integrated approach toward research and outreach will ultimately benefit society, but also improve a scientist's research success.

Each article makes one or more of these aspects of collaboration explicit. Readers will thus find articles on:

Venue and settings: Federal agency staff rely on scientists. Charged with protecting public lands Tim Watkins, Abraham Miller-Rushing, and Sarah Nelson, as well as Shauna Marquardt, Mandy Annis, Ryan Drum, Stephanie Longstaff Hummell, Dave Mosby, and Tamara Smith write about the possibilities for collaborations on public lands. Examples demonstrate how partnerships accomplish innovative research with a direct influence on conservation policy.

The National Park Service provides abundant opportunity for biologists and other scientists to engage global audiences in learning, exploring, and even conducting science. Watkins et al. describe unique opportunities, present several examples that highlight the range of activities and lessons drawn from them, and invite scientists to conduct studies in parks and bring their science into the public eye.

Allies for sharing science: Laying out the rewards of teaming up with informal science learning organizations, Carol Lynn Alpert offers some advice about when and how to approach them. When prospective partners begin discussions early in the proposal development process, they increase the likelihood of successful outcomes in funding, implementation, and impact. Alpert provides a strategic planning worksheet.

Tapping into design sensibility: Nick Hristov, Carol Strohecker, Louise Allen, and Martha Merson introduce a set of design principles that lead to thoughtful visualizations offering not only simple and elegant expressions of information but also outlining ways of thinking about science through visual narrative. Teacher-educator Jocelyn Glazier, Katherine Gill, a landscape architect specializing in learning environments, and Betsy Towns, public

Table 1 Possibilities for outreach efforts

Venue	Ally	Investment	Possible outcomes
Parks	Rangers	Extended PD	
Museums	Exhibit designers	Funding and prototyping	
Play spaces	Designers and learning experts	Co-development	
Community	Volunteers	Protocols and training	
Public land for imperiled species	US Fish and Wildlife	Methods and briefings	

artist and curriculum designer, weave together examples that illuminate the interdisciplinary design of landscapes that nurture learners' curiosity and thinking. The design process resolves conflicting priorities in a natural-habitat zoo and lends a structure to an experiential learning lab where students of all ages experience embodied science learning.

Examples from their exhibit and production experiences give a behind the scenes look at what it takes to create stunning displays that spark interest and inquiry as well as build their audience's awareness of larger issues like species loss. Author teams, Denise King, Joyce Ma, Angela Armendariz, and Kristina Yu; and Jennifer Harrower, Jennifer Parker, and Martha Merson elucidate roles for artists, exhibit designers, and scientists in producing visual art for in-person and online consumers.

Investing time: Grounding interpreters and volunteers in questions, methods, data collection, and discussion of results has tangible benefits. Louise Allen, along with co-authors Cynthia Char, Tracey Wright, Nickolay Hristov, and Martha Merson, comment on the principles informing their work and describe the impact when scientists invest in structures to support park rangers' involvement in science and science communication. Julia Parrish, Hillary Burgess, Jake Weltzin, Lucy Fortson, Andrea Wiggins, and Brooke Simmons suggest that generate robust science outcomes can be produced with attention to the expectations for participants' contributions—simplifying protocols at scale and investing more in training and support for complex.

Taken together, these papers remind readers of the possibilities, acknowledge the complexity of partnerships, and offer examples that are realistic for emerging and established scientists. Although outreach is the focus, the links to research, teaching, and service are evident. Partnerships nurture new lines of research and bring new opportunities funding. Partners may help recruit and train volunteers to expand data collection efforts. Partners may model pedagogical strategies that scientists can adopt to increase engagement in their own classrooms. And as a mental health bonus, they may find respite from everyday pressures and rediscover joy and wonder alongside adults or youth exploring science ideas in an informal setting.

Conclusion

In this volume, authors testify that new partnerships require an investment of time and energy and determination. Unfortunately, we do not have the luxury of putting them off for another day; basic research is under attack now (Zimmer 2018). As scientists seek new partners for outreach and education, all of the authors recommend explicitly discussing expectations. Naming the expected outcomes, audience, funding sources, and time commitments keeps everyone's expectations realistic.

While winning support for a particular line of research might be foremost on a scientist's mind, Besley et al. (2015) have written that scientists who do outreach with the public are more likely to accomplish a broad set of goals. Likely outcomes include:

- Changing perceptions of scientists' motivations/honesty/warmth.
- Increasing excitement/interest/motivation in STEM.
- Changing sense of efficacy related to science learning.
- Increasing knowledge/awareness.
- Reframing how a person thinks about an issue, influencing policy.

These are exciting possibilities. Together we can curate curiosity and entice others to engage. We hope this volume inspires scientists and others to initiate and sustain partnerships in order to place science in the public eye.

Acknowledgments

We three from TERC, Winston-Salem State University, and The Center for Design Innovation express gratitude to colleagues and friends who supported this undertaking. We especially thank the National Science Foundation, the Society for Integrative and Comparative Biology, and the contributors to talks and papers as well as reviewers who gave constructive feedback. We thank Martin Storksdieck for timely and valuable contributions to this introduction. These institutions provided support for the symposium, including: Char Associates, COASST, the Exploratorium, Institute for Learning Innovation, JuniperHarrower.com, the Museum of Science, Boston, the National Park Service, North Carolina School of the Arts, Oregon State University, Tributary Land Design+Build, US Fish and Wildlife Service, University of California Santa Cruz, the University of Minnesota, and the University of Washington.

Funding

The symposium and its proceedings were made possible with support from the Society for Integrative and Comparative Biology, in particular, the Divisions of Animal Behavior, Comparative Biomechanics, Comparative Endocrinology, Ecoimmunology and Disease Ecology, Neurobiology, and Vertebrate Morphology and the National Science Foundation [DRL-123030 and DRL-1514776]. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the view of the National Science Foundation.

References

Besley JC, Dudo A, Storksdieck M. 2015. Scientists' views about communication training. J Res Sci Teach 52:199–220.

Bevan B. 2016. STEM learning ecologies. Issue 1. Research to practice, practice to research. (http://csl.nsta.org/2016/03/stem-learning-ecologies/).

Char C. 2015. To be more inquisitive in the natural world: evaluation of the Interpreters and Scientists Working on Our Parks (iSWOOP) pathways project (http://iswoop-cave.com/?page_id=32).

Firestein S. 2012. Ignorance: how it drives science. New York (NY): Oxford University Press.

Ham SH. 2013. Interpretation: making a difference on purpose. Golden (CO): Fulcrum Publishing Inc.

Holt H. 2017. Channeling scientists. Leg Mag 28:6–8.

Horton CC, Peterson TR, Banerjee P, Peterson MJ. 2016. Credibility and advocacy in conservation science. Conserv Biol 30:23–52.

Irwin A, Wynne B, (eds.). 1996. Misunderstanding science. Cambridge: Cambridge University Press.

Jensen JD. 2008. Scientific uncertainty in news coverage of cancer research: effects of hedging on scientists' and journalists' credibility. Hum Commun Res 34:347–69.

MacDonald B. 2013. Interpreting conservation: communicating about natural resources, scientific research, and critical environmental issues at Cape Cod National Seashore [thesis]. [Amherst (MA)]: University of Massachusetts.

Mayer RC, Davis JH, Schoorman FD. 1995. An integrative model of organizational trust. Acad Manag Rev 20:709–34 (http://www.jstor.org/stable/258792).

McCallie E, Bell L, Lohwater T, Falk JH, Lehr JL, Lewenstein BV, Needham C, Wiehe B. 2009. Many experts, many audiences: public engagement with science and informal science education. A CAISE Inquiry Group Report, 1.

Merson M, Char C, Hristov N, Allen L. 2017. Seeking park-based science information: interpreters at the gate. George Wright Forum 34:368–80.

National Academy of Sciences. 1995. National science education standards. Washington (DC): National Academy Press. Chapter 6, Science content standards. p. 105 (https://www.nap.edu/read/4962/chapter/8#105).

National Research Council. 2009. Learning science in informal environments: people, places, and pursuits. In: Bell P, Lewenstein B, Shouse AW, and Feder MA, editors. Informal environments. Board on Science Education, Center for Education, Division of Behavioral and Social Sciences and Education. Washington (DC): The National Academies Press.

Nisbet MC. 2014. Engaging in science policy controversies: insights from the U.S. debate over climate change. In: Bucchi M, Trench B, editors. Handbook of the public communication of science and technology, 2nd ed. London (UK): Routledge. p. 173–85.

Olson R. 2009. Don't be such a scientist: talking substance in an age of style. Washington (DC): Island Press.

Sacco K, Falk JH, Bell J. 2014. Informal science education: lifelong, life-wide, life-deep. PLoS Biol 12:e1001986 (https://doi.org/10.1371/journal.pbio.1001986).

Selvakumar M, Storksdieck M. 2013. Portal to the public: museum educators collaborating with scientists to engage museum visitors with current science. Curator 56:69–78 (https://doi.org/10.1111/cura.12007).

Stern MJ, Coleman KJ. 2015. The multidimensionality of trust: applications in collaborative natural resource management. Soc Nat Resour 28:117–32.

Storksdieck M, Stylinski C, Bailey D. 2016. Typology for public engagement with science: a conceptual framework for public engagement involving scientists. Corvallis (OR): Center for Research on Lifelong STEM Learning (https://www.aaas.org/sites/default/files/content_files/AAAS_Typology.pdf).

Storksdieck M, Stylinski C, Canzoneri N. 2017. The impact of portal to the public: creating an infrastructure for engaging scientists in ISL. Summative evaluation. Corvallis (OR): Oregon State University.

Zimmer C. 2018. Science and scandal: reporting on science in an age of controversy, Plenary-1, Society for Integrative and Comparative Biology annual conference, 3–7 January 2018. San Francisco (CA).

Integrative and Comparative Biology
Integrative and Comparative Biology, volume 58, number 1, pp. 58–66
doi:10.1093/icb/icy011
Society for Integrative and Comparative Biology

SYMPOSIUM

Unveiling Impact Identities: A Path for Connecting Science and Society

Julie Risien[1] and Martin Storksdieck
Center for Research on Lifelong STEM Learning, Oregon State University, Corvallis, OR 97331, USA

From the symposium "Science in the Public Eye: Leveraging Partnerships" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1]E-mail: Julie.Risien@oregonstate.edu

Synopsis We propose a thoughtful process for scientists to develop their "impact identity", a concept that integrates scholarship in a scientific discipline with societal needs, personal preferences, capacities and skills, and one's institutional context. Approaching broader impacts from a place of integrated identity can support cascading impacts that develop over the course of a career. We argue identity is a productive driver that can improve outcomes for scientists and for society. Widespread adoption of the concept of impact identity may also have implications for the recruitment and retention of a more diverse range of scientist.

Introduction

Over the course of their career, most scientists cultivate an identity aligned to the research they conduct, their contribution to their professional community, and the relationships and partnerships they form within their scientific community. Scientists develop this self-concept and identity by distinguishing themselves from others (mostly non-scientists) through a process of "social differentiation" (Tajfel 1982; Tajfel and Turner 1986). The identity as a scientist is often limited to expressing oneself to professional peers and does not ordinarily connect scientists to public audiences. Here we explore how a narrow perspective on scientists' professional identities has implications for the way the scientific community relates to society. We describe benefits when individual researchers find alignment between their research efforts and public engagement with science. We posit that an expanded professional identity, which we refer to as impact identity, can enable researchers to find a productive way to leverage their research for a broader common good and make strategic and efficient use of a growing system of support mechanisms at the intersection of science and society.

Here we use the terms "scientists" to encompass those who investigate natural and physical phenomena. However, we maintain that these concepts are relevant to engineers, computer scientists, social scientists, and interdisciplinary and applied scientists. We use "success" in two ways with implicit meanings. With regard to broader impacts, success is still quite subjective and the topic of ongoing study and evaluation; for our purposes success refers to situations in which scientists and audiences engaged in science perceive a benefit from broader impacts activity. The concept of a successful scientist differs between disciplines and institutions, and evolves over time. In general, we consider a successful scientist is one who is considered successful by their peers.

Impact identity results from a thoughtful and intentional integration of a scientist's multidimensional self-concept. It blends the researcher, someone who aims at contributing knowledge within a scientific discipline, with the engaged scholar, or someone who ensures results of this research benefit society. Impact identity incorporates a scientist's discipline and scholarship; personal preferences, capacities, and skills; institutional context, and the various communities or social settings in which s/he participates. By integrating these various aspects of a scientist's skills, interests, and opportunities, we expect that a well-developed impact identity can foster approaches to broader impacts that result in better outcomes for the scientist and for society. For scientists, this manifests as more rewarding experiences conducting public engagement in a way that represents them as a whole person. The experiences of public audiences who take part in these public engagement activities should also be improved.

Unveiling and applying impact identity is certainly not enough to achieve high-quality broader impacts. Scientists must also assemble, and make use of, a supportive structure of partnerships and relationships that enable broader impacts success. Fortunately, a growing number of professionals at universities and organizations that engage the public can serve as brokers who help scientists develop relationships and skills and garner the resources necessary to explore the best ways to achieve broader impacts. Well-developed impact identities can serve as a glue between scientists and those who support them, allowing scientists to choose between the myriad of options that exist for connecting public audiences to their research (Storksdieck et al. 2016).

In the sections below, we ground the concept of impact identity in relevant theory about the social boundaries between science, as a subsystem of society, and other sectors of society. We consider the way the scientific enterprise is situated in society; both demarcated from, and in fluid dynamic exchange with, other sectors of society. We then describe societal impacts of research in terms of broader impacts, focusing on the current funding and professional landscape of science, particularly as it applies to the National Science Foundation (NSF). We include two examples of scientists with well-established impact identities. We end with principles for understanding critical dimensions of scientists' identities and an approach to developing impact identity that can help move forward or advance their broader impacts work.

Science and society: theory to inform impact identity

While we live in a "golden age of science" with extraordinary rapid scientific discovery, we are also experiencing anti-science activism that is couched in a narrative of scientists and science as the "other", apart from society and its interests (Hockfield 2018; Holt 2018). Anti-science attitudes play off established social phenomena demarcating the scientific community from non-science realms of society in a way that bestows scientists with authority on scientific process and knowledge about natural and physical phenomena (Gieryn 1983). Assigning authority to a professional class is not limited to science, but is something that is just as true for lawyers, physicians, electricians, and most other professions. The "boundary" between science and other sectors of society is maintained, in part, by strong scientific identities and social interactions that maintain distinctions between groups (Tajfel and Turner 1986). Such boundaries and identities between the realms of science and non-science have been a topic of interest and study for decades (Gieryn 1983, 1995, 1999; Abbott 1995, 1988; Ibarra 1999; Lamont and Molnár 2002; Weingart and Lentsch 2008; Franzen et al. 2012; Clarke et al. 2013).

The demarcation between science and non-science protects the integrity of systematic scientific investigations that build knowledge about the world (Weingart and Lentsch 2008). On the other hand, strong identities and social boundaries come with distinct practices and worldviews that can isolate the scientific community from other sectors of society (Abbott 1988; Gieryn 1995; Seo and Creed 2002). One prominent example where science integrity and norms clash with other sectors of society is the conflict about whether to teach creationism, intelligent design, or evolution in schools. This conflict over which group can claim authority on how we should educate children in the core principles of the life sciences pits science against religion (Brooke 1991).

Maintenance of social boundaries between an expert community and society comes as a cost. For instance, the typical forms of communication, including the use of expert language in peer-reviewed journal articles that themselves are mostly inaccessible to non-scientists limits non-scientists' access to the resources and knowledge of science (Lamont and Molnár 2002). Again, this phenomenon is not limited to science, but it reduces opportunities for the public to engage in meaningful science experiences and for scientists to engage with the public. Fortunately, boundaries between the realms of science and non-science are unstable, always shifting, and being redrawn (Gieryn 1983, 1995), as citizen science powerfully demonstrates (Bonney et al. 2014). Professional identities also shift when individuals experiment with different professional selves (Ibarra 1999; Clarke et al. 2013). Scientists are increasingly required to engage in activities that show the societal impact of their research. Scientists can more easily engage with the public, and vice versa, when they see themselves as part of a larger societal whole, rather than apart from it. Blurring boundaries, and thus integrating science as part of society, therefore opens scientists to potentially rich and innovative exchange with non-scientists (Engeström 2009; Wenger-Trayner and Wenger-Trayner 2015).

Broader impacts and the science funding landscape

Over the last several decades there has been a steady decline in the portion of the federal budget allocated to research (Office of Management and Budget [OMB] 2017), increasing the sense of fierce competition for funding among scientists (Mervis 2017). Meanwhile, the NSF has expanded proposal requirements beyond intellectual merit, explicitly requiring broader impact plans to address societal benefits of the federal research enterprise (National Science Foundation [NSF] 2014). The term broader impacts encompasses a wide variety of potential activities, partnerships, and processes that may enhance the societal benefits of funded research. The NSF explicitly avoids prescribing activities that qualify as broader impacts. Nonetheless, it provides examples such as enhancing public safety, national security, economic prosperity, science learning, broadening participation in the scientific enterprise, and public engagement with science. Although broader impacts include a wide array of activities, outreach and public engagement tend to dominate in fields such as biology, ecology, astronomy, or physics where commercialization is of less importance. Incidentally, the NSF is not the only science agency to pose such challenges to the scientific community. Medical research funded by the National Institutes of Health fits along an implied impact pathway from bench to bedside, with an ultimate goal of improving human health. Department of Education funding similarly aims at improving teaching and learning. Agencies such as NASA and NOAA tie funding to mission success. The NSF broader impacts criterion achieved a new significance over the last few years, though. Expectations for the quality of broader impact component of NSF proposals have increased considerably, elevating broader impacts as a funding criterion from a marginal consideration to one highly relevant to funding success (National Alliance for Broader Impacts [NABI] 2018).

Many scientists piece together a patchwork of broader impacts activities across several programs and grants, addressing them more as a required box to check than an integral aspect of their professional work (Malcom 2018). However, a widely untapped opportunity exists for researchers to instead expand their professional identities and build a legacy of impacts over the arc of their science career, similar to what successful researchers already do with their research portfolio and research direction. Building one's impact identity and developing a portfolio of complementary projects can feel out of reach and under-supported. Lack of professional preparation, mismatched institutional reward structures, and norms of practice within disciplines are common barriers to systematically addressing broader impacts as an integral part of research itself. Many scientists overcome these constraints through bootstrapping, managing to develop the necessary partnerships that help them create successful broader impacts activities (Risien and Nilson 2018). Below are two examples of seasoned scientists who integrated the many dimensions of their identities in order to develop outreach and engagement activities that fit their interests, capacities, societal needs, and research. They both started with modest projects built out of initial partnerships. As they have developed in their careers, those modest beginnings gave rise to a series of increasingly impactful projects, each growing out of the success of the previous. Both scientists have made commendable contributions by blurring the boundaries between science and other sectors of society. They leave in their wake a legacy of broader impacts.

Building the trail of time with underrepresented students

The Trail of Time Exhibition is a fully accessible three-mile-long interpretive timeline trail along the Grand Canyon's south rim that interprets the nearly 2 billion years of Earth's history preserved in Canyon rocks. The trail represents the final product of a systematic effort around broader impacts by University of New Mexico geologist Dr. Karl Karlstrom. He began researching in the Grand Canyon in 1983. A decade later, Karlstrom, his colleague Dr. Laura Crossey, and others wanted to use their emerging research findings to enhance public science literacy around Grand Canyon geology. They recognized that the canyon offered a unique opportunity for visitors to immerse themselves in geology. They started with simple questions about what park visitors may, or may not, be learning about geology. To establish the mechanisms to answer this question they cultivated partnerships from "the top" with park superintendents and from "the base" with park rangers. They worked to collaboratively build their long-term impact plan through a consensus process with partners, along the way bringing underrepresented students into this work. The plan focused on where the goals of scientists, park rangers, and administrators overlapped. Following an NSF planning award, the partnership eventually secured significant funding to develop and build the exhibition. By then the team included academics, students, park interpreters, museum evaluators, and exhibit design specialists. The exhibition opened in 2010 and soon after received an award from the National Association for Interpretation. The team now continues to use trail of time for research on learning and teaching in formal and informal contexts. A logical extension of the geologists' identity as scholars to researchers on how people learn geology. They also work to export the concepts behind trail of time to other parks and educational venues throughout the Colorado Plateau.

The enduring installation is not the only success of their commitment to achieve broader societal impacts with their research. Along the way, Karlstrom and Crossey took on the role and responsibility to mentor several underrepresented students through their transition from undergraduate to graduate studies. They helped students develop personal and professional networks that enable students to more fully participate and progress in their education. This story highlights the years of persistence and ample energy to cultivate partnerships. With initially limited resources, the team was able to create an effective and enduring geoscience experience. Along the way, they provided many of students with motivation to connect their own scientific inquiry to effective public outreach. The story also highlights the extension of the geologists' identity as scholars in geology to becoming scholars of geology learning for all.

Cascading impacts of reconnecting people with trees

Dr Nalini Nadkarni's personal mission is to engage those with no access to forests in learning about forest ecology. Early in her career Nadkarni was struck by how most science outreach "preaches to the choir" and only involves those already interested and engaged in science learning activities. Nadkarni's strong sense that learning about forests and plants should be available to all made her decide to reach new audiences in unexpected places. One group, not commonly considered as an audience for science, is the more than 2 million inmates in the nation's prisons and jails. Early on Nadkarni visited inmates and shared her enthusiasm for science and her love of forests. These visits opened a world of possibility; she enlisted the prison system as partner, and engaged inmates as co-producers to cultivate mosses to repopulate Pacific Northwest forests affected by destructive moss collection for the floral industry. This work led to a sustainability lecture series at the prison, which led to sustainability programing in the prison, and prisoners raising endangered tree frogs to support wild populations. Hers is a story of cascading impacts that are possible when a scientist integrates several dimensions of their identity in their professional life. Nadkarni has spent a career studying trees and contributing to understanding the value of the canopy ecosystem. She also cultivated necessary tools and partnerships to engage those with little access to nature as part of her sense of social justice and her deep belief in the beauty and fascination that forests hold even for those who cannot visit. Her journey centers on her goal of finding common ground with audiences who have little access to science, and who may not value science unless they experience authentic encounters in which scientists care.

Karlstrom and Nadkarni's stories serve as examples of successful scientists with strongly developed impact identities. They have done their broader impacts without sacrificing intellectual integrity or disciplinary standing. They have instead leveraged scientific success as an asset to enhance their impact. Karlstrom and Nadkarni derive substantial personal and professional satisfaction from their impacts work. A stark contrast to many scientists for whom fulfilling broader impacts is intimidating or may feel like a chore. For Karlstrom and Nadkarni broader impacts work emerged from an integrated identity; it served them both professionally and personally. They were both able to build partnerships to pave their way to success. They also played the long game, starting modestly and building from small-scale early successes. In this way, they managed to avoid the piecemeal effect of disjointed broader impacts projects that do not strategically connect with a scientist's research, or with their emerging professional impact identity. Scientists like the two highlighted here serve as the inspiration for developing the concept of an impact identity. In the following section we elaborate on the concept, its elements, and processes scientists can use to develop their impact identities.

Unveiling impact identity: from exploration to action plan

In 2012, various universities were embarking on processes to identify the specific tools and supports scientists and engineers need to effectively design, implement, and evaluate quality broader impacts.

Eventually forming the National Alliance for Broader Impacts (NABI), with funding from NSF, this community now has nearly 700 members who collectively are refining practices that aid scientists in their broader impacts work (J. Risien, submitted for publication). Despite increasing resources, such as training and broader impacts offices, many scientists still tend to rely on limited networks and processes to develop their broader impacts while feeling underprepared to expand or improve their broader impacts work (Risien and Falk 2013; NABI 2018). Nonetheless, demand for broader impacts support is on the rise and professionals who support broader impacts receive frequent requests for "just in time consulting" to help scientists develop broader impacts plans for proposals. This practice can bolster quality of broader impacts plans by connecting researchers to partners and often well-established and adequately evaluated programs to fulfill proposal requirement. However, this approach also positions the principal investigator as a passive actor who outsources broader impact work in order to concentrate on the research aspect of their grant. All too often, this represents a missed opportunity to cultivate skills and align the nature of their research, personal interests, strengths, and institutional capacities with broader impacts. While *ad hoc* solutions to broader impacts fulfillment can have positive outcomes, we argue that a more systematic approach lies in deeper engagement of the researchers themselves. Unveiling and nurturing scientists' impact identity is a critical component of a broader impacts strategy.

"Unveiling your impact identity: fueling your passions and mapping your assets" was a workshop. It was developed to help scientists: 1) explore the many dimensions that together make up their "impact identity"; 2) establish career-long impact goals; 3) identify personal and professional assets that support those goals; and 4) develop a plan to cultivate a toolset to achieve those goals over the long-term. In order to explore these four goals, participating scientists listed scientific issues and research questions about which they feel passionate. Then they recall the point in time when their decision to pursue a career in science was clear, but still unadulterated by concerns of publication rates and career advancement. Next, participants consider the multidimensionality of their own identities, including, but not limited to their identity as researchers, communicators, citizens, as educators, inventors, family members, hobbyists, etc. Identifying one's various self-concepts expands the scientists' frame of reference about skills, interests, and capacities beyond their focused area of research. The various dimensions of identity are examined in order to find connections between research interests and other parts of the scientist's personal experiences. This approach is based on studies which show that scientists are best able to conduct public outreach when they align their (scientific) agendas with expectations of prospective audiences; are part of a systematic effort to reach audiences, receive training, and support; and can build off of initial investments in outreach activities (Selvakumar and Storksdieck 2013; Storksdieck et al. 2017).

The deep-dive into impact identity includes five critical elements, each described below, that participating scientists explore with their participating peers.

(1) Personal identities and intrinsic motivators make up the personal preference dimension. Are you a parent, musician, minority woman in science? Do you enjoy working with children, youth, or adults? Do you see yourself as communicator, teacher, or inventor? Are you an activist, environmentalist, engaged in civic action?

(2) Individuals have certain capacities and skill sets that are somewhat innate or have been cultivated over time, and can guide the type of public engagement that might most suitably fit with a scientist's personally traits and interests. Are you a patient listener? Are you equipped to work with underserved audiences? Do you engage well with children? Are you an introvert or an extrovert? Can you explain your research to lay audiences?

(3) One's approach to research and scholarship adds a dimension that is deeply connected to the everyday professional practice of scientists. Through broader impacts, scholarship often expands beyond the boundaries of a discipline or the core of a research portfolio. What is the nature of your research? What instrumentation do you use? How applied, practical, or theoretical is your research? What are the links between your research topic and potential applications? How might your broader impacts work open new dimensions of scholarship? To what degree might connections outside your circle of disciplinary colleagues support your career trajectory?

(4) Institutions also have identities and scientists do their work within the context of the institutions they inhabit. To what degree does your institution appreciate, support, and reward investments into broader impacts work? Does your

institution have a public service or outreach mission? How is your institution connected to various local or regional communities? What kind of infrastructure exists through your institution to support what type of broader impact efforts (e.g., office of commercialization; institutional connection to local schools or science museums; public speaker or science café/pub series; opportunities to influence policies, legislation, or regulations; etc.)?

(5) Disciplines of science are a major contributor to scientists' professional identities. Affinity with and connection among a disciplinary group is often a prominent dimension of identity. What critical questions drive your discipline? To what degree are fundamentals of your discipline already part of a K-16 curriculum? What are norms within your disciplinary society around broader impact work? How do your successful colleagues conduct their broader impacts?

We posit that ideal impact identity sits at intersection of these dimensions (Fig. 1). As part of creating a personal impact plan for their research, participants in the workshop explore, discuss, and record the various areas of overlap between these five key dimensions of identity to hone in on their individual impact identity. An important sixth dimension accounts for known or perceived societal needs. Researchers are encouraged to think broadly about the societal benefits of their particular research, acknowledging that not all research portfolios easily translate into direct benefits beyond contributions to the scientific knowledge base.

Broadly speaking, researchers explore three basic questions through the workshop. Examining the overlap between discipline and societal needs leads to the question: why or what about my research may be of interest to anyone outside a group of my scientific peers? In the long run, an engaged scientist may ask: what should or could I focus my research on such that it does benefit society? Exploring the intersection of personal preferences and capacities, researchers can ask the question: what would I love to do that I am also well-equipped to do?

These, or related questions, allow researchers to explore options for impact work that align many dimensions of their identity and acknowledge the contexts within which the scientist operates. This systematic approach builds on the nature of the particular research and discipline. It takes into account the interests and perspectives of target audiences, whether those are peers, policy makers, regulators, product developers, a science-attentive public, citizen scientists, schoolchildren, teachers, or interpreters and educators at science museums or other informal science learning settings (Storksdieck et al. 2016). Scientists ultimately can use a series of inquiries and reflections about the intersections of the dimensions of identity to build an action plan. Scientists use an action plan to articulate how they will cultivate the skills, programs, people, and relationships needed to reach impact-related goals and define concrete steps that foster the development and growth of a career-long trajectory that integrates the needs of science with the needs of society. Designed to help scientists focus their broader impacts work, this approach integrates the intellectual merit and broader impacts of their life's work. It offers an opportunity to establish career-long goals concerning scientific and societal impacts, identify personal and professional assets that support those goals, and learn to cultivate a toolset to achieve those goals over the long-term.

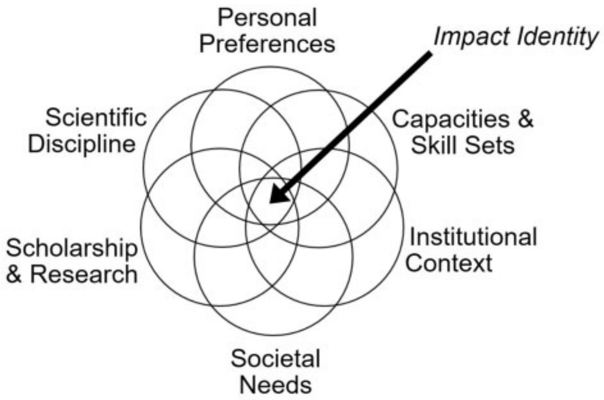


Fig. 1 Multiple dimensions of identity and contexts to explore and integrate in the process of unveiling one's impact identity.

Discussion

Universities, science centers, professional associations, and community organizations are actively developing systems to support scientists in their efforts to strengthen the societal benefits of their research (Risien 2017; NABI 2018; Risien and Nilson 2018; J. Risien and B. E. Goldstein, submitted for publication). *Ad hoc* activities to fulfill broader impacts requirements are being replaced by systematic approaches supported by an emerging university infrastructure and a class of support professionals who specialize in helping scientists fulfill broader impacts requirements. They engage researchers in professional learning that goes beyond outsourcing broader impacts and instead aims at changing capacity and attitudes to help researchers gain a new identity for providing broader societal benefits that emerge from their scientific endeavors (J. Risien, submitted for publication).

Science is an evolving profession and perceptions in the scientific community about professional practice are changing over time. Early career scientists, including graduate students and postdocs, are reportedly enthusiastic and place more value on broader impacts activities (Risien and Falk 2013; Storksdieck et al. 2017; Risien and Nilson 2018). This emerging openness to reaching beyond peers as the sole audiences of one's research activities is developing in parallel with other shifts in norms of the scientific community. For instance, over the last two decades, the advent of team science has shifted interdisciplinary and transdisciplinary science from a novelty to accepted practice (National Research Council [NRC] 2015). Similarly, scientists who engage the public, once looked upon with suspicion by their peers, are increasingly applauded for strengthening the link between the research enterprise and society (Lohwater and Storksdieck 2017). Scientists who are successful in their discipline and achieve notable societal impacts have three things in common. First, they blend disciplinary strength and passion with a deep conviction and commitment to broader societal impacts. Second, they draw on a rich set of partnerships that enable them to engage in practices likely to have meaningful impacts. Finally, their professional identity expands well beyond their discipline or the confines of their research topic. They are able to knit together disciplinary ties, personal relationships, intellectual contributions, and passion for science along with their other interests and strengths to achieve meaningful impacts.

The concepts described above in the process of unveiling one's impact identity have been applied in a handful of workshops of varying length. Evaluations of workshops indicate that researchers experience immediate value, including reduced fear and confusion about broader impacts requirements, expanded understanding of possible broader impacts activities, and excitement for developing a broader impacts trajectory that resonates with them both personally and professionally. There is much to learn about the potential of this systematic identity-based approach. Additional tests of the concepts, iterations of workshop design, formative assessment, and a longitudinal study of participating scientists can contribute to better understanding about the benefits of the approach and help to guide investments of researcher time and institutional resources. We hypothesize that using impact identities as a central organizing principle in developing career-long broader impacts yields benefits to scientists, the public audiences they engage, and enables one to strategically build on modest beginnings of broader impacts efforts.

Enthusiasm for engaging with broader impacts, increased desire for integrating work and life, and a drive to gain competitive advantage in the funding landscape may predispose early career scientists for maximum benefit from impact identity work. However, reports from the NABI community confirm that seasoned scientists are increasingly working to integrate broader impacts into their professional portfolios as well, and may also benefit from dedicated time to unveil their own impact identities, if only to become more deliberate mentors to their younger colleagues.

The NABI community has embraced the concept of impact identity in the trainings they provide to researchers and the professionals that support them. Social science research on NABI as a community has revealed critical practices, which include helping scientists in engaging non-peers in their research, helping scientists imagine ways in which their research supports broader societal goals, and brokering relationships and partnerships required to conduct broader impacts activities aligned with societal needs (J. Risien, submitted for publication). Trained to think within a scientific discipline, and subject to processes of reward and recognition that prioritize research outputs, scientists develop strong disciplinary identities that can isolate them from other sectors of society. Such isolation may stymy development of the skills and partnerships needed to generate a meaningful broader impacts portfolio. This can lead to the common stereotype that the only thing that matters in science is full dedication to research itself, at the expense of all other considerations. The scientific community is fighting this stereotype since it is seen as a barrier to attracting or retaining talent uninterested in a unidimensional identity, as researcher for research sake, and instead prefers to express a multi-faceted identity and incorporate strong societal connections in their professional lives (Eccles and Wigfield 2002; C. Stylinski et al. submitted for publication). At the same time, this stereotype is still part of the lived experience of far too many graduate students, postdocs, and other emerging scientists (Risien and Nilson 2018).

Retaining scientists from underrepresented groups in an effort to broaden participation and productivity of science will require many systemic shifts. Approaching this work from a place that recognizes the importance of allowing individuals to develop an identity as scholar and citizen will tap into ongoing efforts to improve conditions for underrepresented scientists. Programs like NSF ADVANCE prioritize work–life integration, and universities are beginning to hire faculty with position descriptions that explicitly support public engagement. Departments across many universities are already updating their promotion and tenure guidelines to more meaningfully include and assess public engagement (Risien and Nilson 2018). Consequently, we posit that widespread adoption of the concept of impact identity may have implications for the recruitment and retention of a more diverse range of scientist, and ultimately serve as a practical tool to address longstanding concerns about a better integration of science into society (Weingart and Lentsch 2008; Hockfield 2018; Holt 2018).

Conclusion

Just as the boundaries between science and society change, identities are malleable and can shift. They evolve alongside changing norms of conduct and transforming expectations around what counts as success in science. We propose that unveiling impact identities, articulating impact specific goals, and developing long-term plans are critical to broader impacts success and for a satisfying career as a scientist. This entails integrating the many dimensions of a scientist's identity and the many contexts within which scientists conduct their work: their personal preferences, skills, and abilities; disciplinary affordances and scholarship; institutional homes; and the communities they are part of all shape how researchers position their science within and outside of academe. The use of impact identity as a framing concept for professional development holds promise to improve the reach and effectiveness of institutional infrastructures and professional support systems that work to better connect science and society.

Acknowledgments

We thank the Center for Advancement of Informal Science Education (CAISE) for supporting initial investigations that sparked these ideas and our colleagues in the National Alliance for Broader Impacts (NABI) for engaging with these ideas and enhancing them as they apply them in their work to support broader impacts. Thank you to the Society for Integrative and Comparative Biology and to Martha Merson for connecting these ideas to the SICB community. We thank Karl Karlstrom from the University of New Mexico and Nalini Nadkarni from the University of Utah for inspiring us with their stories. Thank you also to Kelly Riedinger for reviewing early versions of this paper.

Funding

This material is based upon work supported in part by the National Science Foundation under Grants *DRL 1612808, DRL 1212803*, and *MCB 1408736*. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

References

Abbott A. 1995. Things of boundaries. Soc Res 62:857–82.

Abbott A. 1988. The system of professions. Chicago (IL): University of Chicago Press.

Bonney R, Shirk JL, Phillips TB, Wiggins A, Ballard HL, Miller-Rushing AJ, Parrish JK. 2014. Next steps for citizen science. Science 343:1436–7.

Brooke JH. 1991. Science and religion: some historical perspectives. London (UK): Cambridge University Press.

Clarke M, Hyde A, Drennan J. 2013. Professional identity in higher education in the academic profession in Europe: new tasks and new challenges. Netherlands: Springer. p. 7–21.

Eccles JS, Wigfield A. 2002. Motivational beliefs, values, and goals. Annu Rev Psychol 53:109–32 (https://doi.org/10.1146/annurev.psych.53.100901.135153).

Engeström Y. 2009. Expansive learning toward an activity-theoretical reconceptualization. In Illeris K, editor. Contemporary theories of learning. New York (NY): Routledge. p. 53–72.

Franzen M, Weingart P, Rödder S. 2012. Exploring the impact of science communication on scientific knowledge production: an introduction. In: Rödder S, Franzen M, Weingart P, editors. The sciences' media connection—public communication and its repercussions. Dordrecht: Springer. p. 3–16.

Gieryn TF. 1983. Boundary work and the demarcation of science from nonscience: strains and interests in professional ideologies of scientists. Am Sociol Rev 48:781–95.

Gieryn TF. 1995. Boundaries of science. In: Jasanoff S, Markle GE, Petersen JC, editors. Handbook of science and technology studies, revised edition. Thousand Oaks (CA): SAGE Publication. p. 393–443.

Gieryn TF. 1999. Cultural boundaries of science: credibility on the line. Chicago (IL): University of Chicago Press.

Hockfield S. 2018. Our science, our society. Science 359:499.

Holt R. 2018. A tale of two cultures. Science 359:371.

Ibarra H. 1999. Provisional selves: experimenting with image and identity in professional adaptation. Adm Sci Q 44:764–91.

Lamont M, Molnár V. 2002. The study of boundaries in the social sciences. Annu Rev Sociol 28:167–95.

Lohwater T, Storksdieck M. 2017. Science communication at scientific institutions. In: Scheufele D, Kahan DM, Hall Jamieson K, editors. Handbook of the science of science communication, Chapter 19. New York (NY): Oxford University Press. p. 179–86.

Malcom S. 2018. Reflecting on our roots—part four broader impacts in NSF includes open forum. Washington (DC): AAAS.

Mervis J. 2017. Data check: US government share of basic research funding falls below 50%. Science Magazine. Mar. 9, 2017.

National Alliance for Broader Impacts [NABI]. 2018. The current state of broader impacts: advancing science and benefiting society. Columbia (MO): National Alliance for Broader Impacts (https://www.broaderimpacts.net).

National Research Council [NRC]. 2015. Enhancing the effectiveness of team science. Washington (DC): National Academies Press.

National Science Board [NSB]. 2011. National Science Foundation's merit review criteria: review and revisions. Arlington (VA): National Science Foundation (http://www.nsf.gov/nsb/publications/2011/meritreviewcriteria.pdf).

National Science Foundation [NSF]. 2014. Perspectives on broader impacts. Washington (DC): NSF. (http://www.nsf.gov/od/iia/publications/Broader_Impacts.pdf).

Office of Management and Budget [OMB]. 2017. Historical tables. Washington (DC): Executive Office of the President, Office of Management and Budget (https://www.whitehouse.gov/omb/historical-tables/).

Risien J. 2017. The national alliance for broader impacts. In: Goldstein BE, editor. Transformative learning networks: guidelines and insights for netweavers. Washington (DC): Network of STEM Education Centers. p. 18–50 (https://serc.carleton.edu/StemEdCenters/178058.html).

Risien J, Falk JH. 2013. STEM principle investigators perceptions and practice of broader impacts: front-end report for the Center for the Advancement of Informal Science Education November 2013 Convening in Washington, DC (http://www.informalscience.org/caise-convening-broader-impacts-and-ise-front%E2%80%90end-report).

Risien J, Nilson R. 2018. Landscape overview of university systems and people supporting scientists in their public engagement efforts: summary of existing recommendations and evidence from the field. Report to the Kavli, Rita Allen, Packard, and Moore Foundations presented March 27–28, 2018 at Support systems for scientists' sommunication and engagement series, workshop 3: academic institutions (http://informalscience.org/support-systems-scientists-communication-and-engagement-exploration-people-and-institutions).

Selvakumar M, Storksdieck M. 2013. Portal to the public: museum educators collaborating with scientists to engage museum visitors with current science. Curator 56:69–78.

Seo MG, Creed WD. 2002. Institutional contradictions, praxis, and institutional change: a dialectical perspective. Acad Manage Rev 27:222–47.

Storksdieck M, Stylinski C, Bailey D. 2016. Typology for public engagement with science: a conceptual framework for public engagement involving scientists. Corvallis (OR): Center for Research on Lifelong STEM Learning (https://www.aaas.org/sites/default/files/content_files/AAAS_Typology.pdf).

Storksdieck M, Stylinski C, Canzoneri N. 2017. The impact of portal to the public: creating an infrastructure for engaging scientists in informal science learning: summative evaluation. Corvallis (OR): Oregon State University (https://popnet.pacificsciencecenter.org/wp-content/uploads/PoPNet-Summative-Evaluation-Report.pdf).

Tajfel H. 1982. Social psychology of intergroup relations. Annu Rev Psychol 33:1–39.

Tajfel H, Turner JC. 1986. The social identity theory of intergroup behavior. In: Worchel S, Austin WG, editors. Psychology of intergroup relations. Chicago: Nelson Hall. p. 7–24.

Weingart P, Lentsch J. 2008. Wissen, beraten, entscheiden: form und funktion wissenschaftlicher politikberatung in Deutschland. [Knowledge, advising, deciding: forms and functions of scientific policy consulting in Germany] Weilerswist (Germany): Velbrück Wissenschaft.

Wenger-Trayner E, Wenger-Trayner B. 2015. Learning in landscapes of practice. In: Wenger-Trayner E, Fenton O'Creevey M, Hutchinson S, Kubiak C, Wenger-Trayner B, editors. Learning in landscapes of practice: boundaries, identity, and knowledgeability in practice-based learning. New York (NY): Routledge. p. 13–29.

Integrative and Comparative Biology
Integrative and Comparative Biology, volume 58, number 1, pp. 67–76
doi:10.1093/icb/icy025
Society for Integrative and Comparative Biology

SYMPOSIUM

Science in Places of Grandeur: Communication and Engagement in National Parks

Tim Watkins,[1,*] Abraham J. Miller-Rushing[†] and Sarah J. Nelson[‡]

*Natural Resource Stewardship and Science Directorate, National Park Service, 849 C Street NW, Mail Stop 2647, Washington, DC 20240, USA; [†]Acadia National Park (US National Park Service) and Schoodic Education and Research Center, Winter Harbor, ME 04693, USA; [‡]School of Forest Resources, Ecology and Environmental Sciences Program, University of Maine, Orono, ME 04469, USA

From the symposium “Science in the Public Eye: Leveraging Partnerships” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1]E-mail: tim_watkins@nps.gov

Synopsis The USA has set aside over 400 national parks and other protected areas to be managed by the National Park Service (NPS). Collectively, these sites attract over 300 million visits per year which makes the NPS one of the largest informal education institutions in the country. Because the NPS supports and facilitates scientific studies in parks, the national park system provides abundant opportunity for biologists and other scientists to engage global audiences in learning, exploring, and even conducting science. Those opportunities are best pursued through collaborations among scientists and the professional communication staff (interpreters, educators, media specialists, etc.) of parks and their partner organizations. This article describes unique opportunities and rationale for such collaborations, presents several examples that highlight the range of activities and lessons drawn from them, and invites scientists to conduct studies in parks and bring their science into the public eye.

Communicating science to public audiences and engaging those audiences in science is a grand challenge for modern society. Scientists support efforts to do so because of the rapid pace of scientific advancements and the need for people to integrate science with personal values when making important life and policy decisions. Communicating science well can be difficult and requires particular skills (National Academies of Sciences, Engineering, and Medicine 2017) so collaborations between scientists and professional communicators are valuable. Given that opportunities to learn science are abundant in out-of-school settings over the course of our lives (National Research Council 2009; Falk and Dierking 2010; Fenichel and Schweingruber 2010) informal learning environments (i.e., media and settings like museums, parks, zoos, and after-school programs) are important venues for scientists to collaborate with professional communicators.

We contend that national parks in the USA are ideal places for such collaboration. They are similar to field stations, long-term ecological research sites, and experimental forests and ranges in that they host thousands of research projects. But national parks receive many more visitors and their mission includes communicating to and engaging with those visitors. Park staff include professional interpreters, educators, and other communicators who serve that mission. Scientists therefore can conduct research in national parks and collaborate with staff to communicate their science or engage the public through a variety of means. Park audiences—including resource managers, school groups, local residents, and the visiting public—actively seek scientific information and welcome opportunities to learn and experience science in parks (Beard and Thompson 2012; Thompson et al. 2013).

Science communication and engagement in science in informal settings is a mature field with its own funding streams (e.g., National Science Foundation’s Division of Research on Learning in Formal and Informal Settings), syntheses (e.g.,

Advance Access publication May 29, 2018
Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology 2018.

National Research Council 2009; Fenichel and Schweingruber 2010), strategic frameworks and guidelines (e.g., Shirk et al. 2012; Bell et al. 2017), and institutional centers. We still have much to learn, as described in the research agenda laid out by the National Academies of Sciences, Engineering, and Medicine (2017). Moreover, while there is some recent literature on effective interpretation and communication in US national parks and other federally protected lands (Stern et al. 2010; Beard and Thompson 2012; Stern and Powell 2013; Thompson et al 2013), it is not focused on science communication and engagement *per se*. Scientists who communicate or engage the public in their field research in national parks therefore have the opportunity to make additional contributions to our understanding of effective practice in these places.

Here we describe how scientists can collaboratively conduct, communicate, and engage the public in research in US national parks. We begin with an overview of national parks' unique value as venues for such activity. We follow that with examples from parks that span a range of methods (from explaining science to an audience to engaging an audience with science; Bell et al. 2017), audiences (general public, teachers, etc.), and scientist roles, and then draw together some lessons that apply generally. We end with comments on the promising future of science communication in national parks and on the emotional values that scientific discovery and national parks have in common.

Throughout, we explore four key messages for scientists interested in bringing their research into the public eye. First, national parks are exceptionally valuable places for research and science outreach. Second, the National Park Service (NPS) has programs and mechanisms to support the work of scientists, including channels for scientists to initiate and grow research and outreach programs. Third, park staff have expertise, ability, and willingness to support the full range of outreach activities. And fourth, scientists can collaborate with park staff as we collectively seek to ensure that research informs management and increases public awareness, understanding, and appreciation for national parks and for science. As we previously alluded, not enough is known about science learning in national parks, including the roles of scientists themselves. The NPS wants and needs to understand more.

Parks for research, communication, and engagement

The NPS actively conducts and welcomes research by its own staff, other government scientists, and academic researchers (Sauvajot 2016). Its policy is to use best available science to inform management, encourage research studies, cooperate with educational and scientific institutions, and provide facilities and assistance to researchers (National Park Service 2006). It applies this policy to the 417 units (national parks, monuments, seashores, lakeshores, battlefields, historic sites, etc.) across all US states and territories. Given this policy regarding science and the legal mandate of the NPS to preserve places "unimpaired for the enjoyment of future generations," national parks are permanently protected long-term research sites with documented natural, cultural, and management history. That documentation includes research reports, data, field notes, maps, specimens, and other records maintained in museums and archives and searchable online (irma.nps.gov, museum.nps.gov, and npgallery.nps.gov).

To study in national parks, researchers must submit proposals and apply for permits (irma.nps.gov/RPRS), a process that begins relationships with park resource managers, research coordinators, and interpreters. In 2017 the NPS issued 2990 research permits. Topics ranged widely across social sciences (e.g., visitor use patterns), cultural sciences (zooarchaeology of ancestral Puebloan settlements), earth sciences (snow persistence and alpine stream hydrology), ecology (faunal responses to rapid climate change), evolutionary biology (zooplankton speciation), and so on. Several permits were also issued for educational purposes like undergraduate field courses, macroinvertebrate inventories and water quality testing by high school students, and collection of fish specimens for educational displays at a public aquarium.

In addition to being places for research, national parks have unique value for communication and public engagement with science. They are among the most inspiring and unique places in the world, and have been set aside for all people to enjoy. They are sources of pleasure and thus are exemplary places of "learning for fun" (Packer 2006). When visitors to a park encounter science that helps inform that park's—their park's—preservation, they have the chance to understand the science and discover its relevance to their lives—a phenomenon known best from research in science museums, centers, zoos, aquariums, and other places where people expect to encounter science (Schwan et al. 2014). Scientists who conduct research in national parks therefore can place their science directly into a personal and civic context and engage a highly interested and receptive audience who are experiencing positive emotions (National Research Council 2009; Rogoff et al. 2016).

The thousands of NPS interpreters and other communication professionals draw on special attributes of parks to help visitors build emotional and intellectual connections to these places (Stern et al. 2010; Larsen 2011). They are experts at telling stories in person and through media that enrich the visitor's experience. The services they provide likely contribute to the consistently high ranking of the NPS among federal agencies in polls of the American public (Pew Research Center 2015). The combination of emotionally appealing public places, well-liked communicators, and breadth of geography and natural–cultural systems available for *in situ* research is not found among zoos, aquariums, museums, after-school programs, or other informal education settings. With over 300 million visits annually, plus over 90 million web visitors and several million social media followers, the NPS in collaboration with scientists has tremendous potential to foster science learning worldwide.

Programs to support research and public engagement in parks

Most national parks work with scientists on research and communication activities. The relationships that are established through the permit process enable every permitted scientist to express or respond to interest in communicating science to various audiences. Scientists can use the application form to propose standalone education and outreach activities (e.g., teaching a class) or communication components of a research project. A park may even make outreach and communication a condition of the permit.

The NPS has established two programs that facilitate research and science communication beyond the relationships established through the permitting system. Research Learning Centers (RLCs—nps.gov/rlc) are located in several parks across the country. Their staff assist with all aspects of science from proposal development through the conduct of research and communication of results. Most RLCs provide housing, work space, computer network access, access to publications and collections, logistic support, and some equipment. Cooperative Ecosystem Studies Units (CESUs—cesu.org) facilitate research, education, and technical assistance partnerships among federal agencies and US universities and other non-government organizations. They enable scientists to learn about research opportunities in parks and move federal funds to scientists for projects that meet park needs. The NPS employs research coordinators who work at the CESU host universities and regularly match parks with institutions or individual scientists to collaborate on projects.

A typology and examples of science communication and engagement in parks

Storksdieck et al. (2016) created a typology of approaches to public engagement with science that can help scientists and other practitioners align their actions with their goals, skills, and interests. The typology uses a set of variables to distinguish among approaches: size, structure, form and depth of engagement, the dominance and authority of the scientist versus others in the audience, interactions between scientists and participants, etc. National parks host science communication and engagement activities that span much of the range described in the typology. Below, we provide examples that illustrate the range from "low hanging fruit" of explaining science to an audience to the "high-hanging fruit" of engaging an audience via contributory citizen science. All our examples illustrate behaviors and attitudes that Storksdieck et al. (2016) identify as critically important: a genuine curiosity about the public; the willingness to listen and learn from audience members; an ability to perceive and respond to the audience's need for information and detail; and a willingness to make personal connections with audience members. Those behaviors and attitudes are exhibited to one degree or another by scientists; they are also elicited, fostered, and mediated by NPS communications professionals whose knowledge and skills complement those of the scientists.

Example 1: Contributing to science communication by others

Scientists can advise, review, or otherwise contribute to products made by NPS communications staff. Such collaboration can take little time investment, may be done in or out of a park (e.g., from one's office), and may not require specialized communication skills beyond the writing, reviewing, and speaking that scientists already perform daily. One example is a US Forest Service bat ecologist doing research in Congaree National Park who fact-checked and reviewed summary documents the park's RLC staff had created for public audiences about her research (nps.gov/rlc/ogbfrec/bat-research.htm). She also presents occasionally to park staff and the public during a casual seminar series in the visitor's center. A second example involves biologists from the University of California who conduct research in Yosemite and Sequoia-Kings Canyon National Parks and Point Reyes National Seashore. They explained their studies on camera for short videos about ocean acidification and species range shifts. The videos were produced by one of us (T.W.) and an undergraduate student for online distribution to the general public (nps.gov/climatechange) and NPS interpreters who were being professionally trained in climate change communication. The scientists were brought to our attention by the CESU research coordinator and RLC staff who liaise regularly with UC faculty.

Both of these examples emphasize traditional communication of science to audiences rather than two-way engagement of audiences with science (Bell et al. 2017), though some engagement and mutual learning occurred during the live seminars and during the video production process. In the typology of Storksdieck et al. (2016), these examples involve small group sizes, in-person and online forms of engagement, an overt science focus, the dominance of the scientist's voice, and heterogeneous adult audiences. Beyond measured outputs (e.g., numbers of attendees at seminars, web article pageviews, or video plays), the NPS and collaborating scientists know little about the impact of their communication on audiences' knowledge or attitudes about science or parks.

Example 2: Scheduled public outreach event in a park

A "higher-hanging fruit" opportunity involves engaging public audiences directly through an outreach event planned, organized, and directed by park interpreters and other communicators. Some parks offer science festivals and related outreach events during which scientists can engage visitors. For example, at Indiana Dunes National Lakeshore, RLC staff organize "Indiana Dunes, Science, and YOU!" on a Friday for school groups, and again on Saturday for the general public. On both days, scientists present their research in an auditorium with discussion moderated by RLC staff. The sessions with school groups also include discussions about what it is like to be a scientist. After the presentations the scientists take participants, with staff and teachers, into the park where they elaborate on their research, demonstrate field methods, and guide participants in using equipment and collecting data. Topics have included the processes of dune movement, bacterial contamination of Lake Michigan beaches, and the preservation of a federally threatened plant species. Because these topics are related to conservation of the park and to the visitors' enjoyment of it, they are germane to the interests of local residents who frequent the park.

To conduct this event, NPS communicators and scientists spend a few hours preparing and collaborating in advance. The RLC staff recruit scientists who they know are good communicators and whose research is inherently interesting to the public. They provide specific guidance and skill-development for communicating with adult and teen audiences, support for field activities, and feedback on draft presentations and plans. The scientists create their presentations and field activities, organize field equipment and supplies, and share their enthusiasm for research.

Compared with Example 1, face-to-face outreach described here is an example of engaging the public with science rather than simply communicating science to the public. In the Storksdieck et al. (2016) typology, this event involves larger audiences, is done in-person with a balance of scientist and public voices, involves more support from the communications expert, and engages the audience through demonstrations, data collection, and field expeditions.

Consistent with the professional craft of NPS interpreters and science communicators, this face-to-face activity is at heart a dialog in which "publics and scientists both benefit from listening to and learning from one another" (Bell et al. 2017). While rigorous evaluation and research on outcomes has not been conducted, feedback from participating scientists and teachers reveals that this type of event allows the public to talk and share views about how they relate to science, and the scientists to develop and refine their communication skills.

Example 3: Planning for communication in a research project

The previous examples illustrate science communication and public engagement that emerges after a research project is underway or complete. Communication can also be intentionally included, and funded, in a research project from the outset. Doing so entails sustained collaboration between scientists and communications experts, delineation of roles, and recognition of each other's expertise.

"Changing Tides" is a three-year study of how brown bears forage and use resources in the intertidal zones at Katmai and Lake Clark National Parks in Alaska (nps.gov/katm/learn/changing-tides.htm).

It involves biologists from NPS, US Geological Survey, Washington State University, and other institutions and science communication experts from the RLC that serves the two parks. The communications work was supported by undergraduate communications interns hired by the RLC who collectively provided direction and guidance to senior scientists and graduate student researchers. Because the parks are remote the team developed digital products: the project website with links to a "scientist in the field" blog and an interactive story map, emailed newsletters, YouTube videos, Facebook posts, and a live online chat with project biologists. These resources were also incorporated into a high school teacher training workshop conducted by RLC staff with involvement of the lead scientist.

The RLC staff led all communications activities during the project and had co-PI status. The biologists collaborated by responding to draft communication plans, advising on key science messages, and accommodating communication logistics. They sat for video interviews, wrote blog entries, fact-checked newsletters, explained their science and offered stories from the field in the teacher workshop, and provided datasets that teachers and students use in class.

With the exception of the teacher's workshop, communication was mostly unidirectional. In the typology of Storksdieck et al. (2016), the audience was very large and heterogeneous, the engagement was online, the focus was overtly scientific, the voice and authority was centered on the scientist rather than the public, and the research was basic but with strong implied societal dimensions (e.g., conservation of an iconic and economically valuable species). The live online chat, Facebook posts, and blog comments allowed some synchronous and asynchronous two-way conversation with public audiences. Impacts of the web-distributed products (as opposed to outputs like number of pageviews) were not assessed. Teachers at the workshop placed very high value on the products and indicated they would use them in their teaching. They also specifically valued the presentation by one of the scientists, the opportunity to get to know him, and to hear his stories about his professional life as a field researcher (J. Pfeiffenberger, personal communication).

Example 4: Training and practice in science communication

In 2016, NPS partnered with the Association for the Advancement of Science (AAAS) and Schoodic Institute (a close science partner of Acadia National Park) in launching the Second Century Stewardship initiative (SCSParkScience.org) to encourage science that informs conservation decisions and engages the public. It provides early-career scientists (Ph.D. students, post-docs, and junior faculty) with three benefits: (1) competitive funding for innovative research in national parks; (2) training and opportunities to enhance learning and engagement of students, educators, and the broader public; and (3) opportunities to inspire and inform stewardship of our natural and cultural heritage. The initiative began at Acadia National Park and will expand to more parks in the near future.

A key feature of the program is a workshop (with about 25 attendees in 2017) that provides research fellows, NPS staff, and professionals from partner organizations with training in a variety of communication methods—presenting to the public; writing magazine articles and blogs; recording podcasts; posting social media with the hashtag #ParkScience; creating videos; and briefing officials. Outside experts (e.g., professional video producers, social media experts, and public affairs officers) provide specific training, and the fellows bring their own expertise, curiosity, and enthusiasm.

The intent is not that all attendees become proficient in all of the skills, but rather that they get exposed to them and then focus on the techniques and media most appropriate for their interests, abilities, and goals. Most of the attendees in 2017, for example, did not have Twitter or Instagram accounts before the workshop, nor had they written blog posts or recorded videos about their work. All of the fellows said that the workshop turned them on to communication strategies they would not have considered before (e.g., videos and social media), and they are all communicating much more now than they would have without the workshop.

These workshops do not directly engage the public, but rather give selected participants the skills to communicate and engage the public in science using methods across the typology of Storksdieck et al. (2016)—big or small programs, in-person or remote engagement, and in-depth or minimal engagement (e.g., citizen science or a tweet). One important aspect of public engagement with science is the practice and refinement of scientists' own communication skills (Bell et al. 2017), which is an explicit goal of the SCS initiative.

Example 5: Citizen science in parks

The Dragonfly Mercury Project (DMP: nature.nps.gov/air/Studies/air_toxics/dragonfly/) is a citizen science initiative focused on accumulation of airborne mercury in aquatic biota. Scientists from the University of Maine, US Geological Survey, and the NPS collaborate with park staff who lead citizen scientists (mostly middle and high school groups, as well as community volunteers; Fig. 1) in collecting dragonfly larvae and submitting them for mercury analysis. The DMP began in 2012 as the feasibility of citizen science became more apparent and as new technology enabled inexpensive analysis of tissue mercury (e.g., Nelson et al. 2015; Eagles-Smith et al. 2016). The project launched in 11 national parks and has grown to involve more than 90 parks and 3000 citizen scientists nationwide.

The DMP started in response to State and Federal funding for science teacher professional development in Maine. It is now funded by the NPS, with individual parks paying for materials and supplies needed to participate. Based on relationships cultivated during a decade of research in Acadia National Park, one of us (S.J.N.) collaborated with Schoodic Institute and teachers across northern New England to develop and test protocols for sampling aquatic invertebrates, resulting in a co-created pilot effort (Shirk et al. 2012). Subsequent collaboration with NPS Air Resources Division experts enabled us to expand to additional parks and engage more scientists to extend the scope and capabilities of the research team. As the project expanded to ∼25 national parks, it became more of a collaborative model (Shirk et al. 2012), in which staff at those parks helped refine communication and outreach materials.

The DMP adapts Zoellick et al.'s (2012) framework for formal science education to the informal setting of national parks: scientists and NPS staff share roles in the project's design and implementation, but their goals and desired outcomes diverge. NPS goals often focus on connecting people to parks whereas scientists' goals focus on collecting and interpreting data. Citizen science collection events allow both scientists and park staff to share the implementation of this program, and yield outcomes that are meaningful for scientists, citizens, and the parks. Parks commonly report success at getting kids outside, which meets those parks' biodiversity discovery goal (Flanagan Pritz and Nelson 2017). And the scientists benefit because without local citizens who collect samples, they would not be able to get data from 90+ parks around the country.

In the typology of Storksdieck et al. (2016), the DMP generally exemplifies more intensive interactions: small groups are engaged in-person by a professional practitioner and/or scientist for several hours to a day (or days) in collecting, identifying, and preparing samples. The activity is overtly about science, with groups ranging across ages and genders (Flanagan Pritz and Nelson 2017), and with interactions that generally allow for all voices to be heard and questions to be asked by participants. In many ways, the DMP is an example of public participation in research (i.e., co-production of knowledge). It deviates from the example in Storksdieck (2016) in that communication with the public is mediated by NPS staff in most cases. However, many NPS staff who participate in the project and lead citizen groups in the field are themselves scientists, or have training and degrees in science.

Lessons learned

From the examples above we extract some lessons about science communication in parks and factors that promote successful collaborations between biologists and NPS staff and partners. Readers may identify and draw additional meanings.

Researchers in parks may encounter visitors who ask them about their work: Even if public outreach is not part of a study plan, scientists should talk in advance with park staff about responding to public interest. The bat ecologist working in Congaree, for example, often speaks with visitors who are curious about her radio telemetry equipment. She embraces the unplanned outreach opportunities and collaborates with RLC and park staff to make the most of them. Often researchers in parks cite these interactions as unexpected bonuses—positive interactions with park visitors reinforce the value of their work and expertise. Such interactions can carry a cost, however, as they can disrupt field work if they are too frequent. The key is to communicate clearly with the public and get park staff assistance on managing visitors' engagement. The SCS initiative provides fellows with training on how to manage such unplanned interactions without compromising their ability to do their research.

Success in outreach may depend on the relationships that scientists and park staff establish: Not all scientists are skilled at communicating with the public. Research on interpretation in national parks (Stern and Powell 2013) shows that positive outcomes for visitors are correlated with program qualities (e.g., good organization, relevance to audience, links to intangible ideas and emotions) and presenter qualities (e.g., confidence, authentic emotion, humor) that require training and practice. NPS communicators have and routinely employ those qualities. When good relationships allow those qualities to

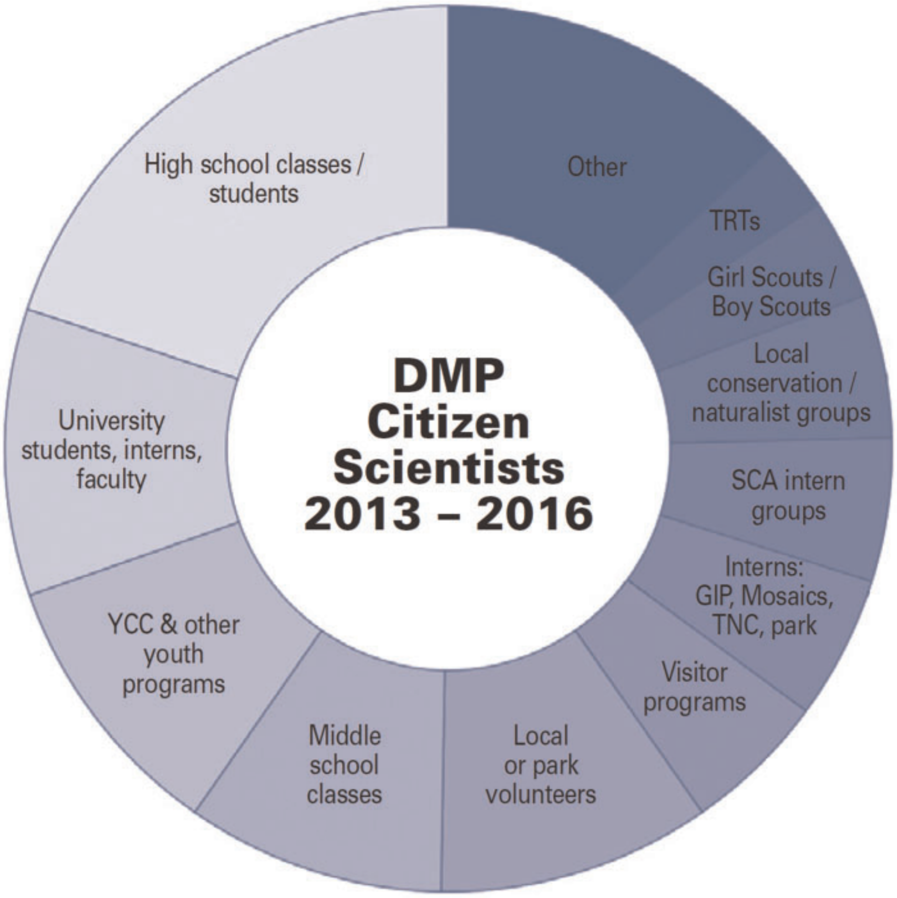


Fig. 1 A wide range of local participants was engaged in the dragonfly citizen science project through national and local partners. TRT, teacher ranger teacher; SCA, student conservation association; YCC, youth conservation corps; GIP, geoscientists in parks; TNC, the nature conservancy. Courtesy of Maine Policy Review. Reprinted with permission.

be combined with the deep content knowledge, enthusiasm, and other characteristics of scientists, communication and engagement is successful. The complex and well-received products of the Changing Tides project were possible because the RLC communications staff and research scientists related as co-equal professionals and collaborated in all phases of the project. A similar set of co-equal and complementary roles existed among scientists and park interpretive staff in the DMP project. Building the collaborative relationships takes time (including time away from research) but the payoffs are proportional if not greater.

Planning for communication and engagement is important, and it is probably safe to err on the side of too much planning: Both the RLC staff and scientists in the events at Indiana Dunes realized afterward that more practice with public speaking and "dry run" demonstrations in the field would have improved the program, but each was hesitant to take up the other's time before the event. But in a good relationship, all parties can push for detailed information and preparedness without worrying about impinging on each other.

It is important to match goals, audiences, and methods: Researchers in parks commonly file reports with NPS, contribute to brief summaries of their work, or give general talks to park staff, academic audiences, or the public. Where the goal is to inform the awareness or behavior of particular audiences—e.g., to make local residents aware of the damage that non-native plants cause and see the value of planting native species, or to inspire science-interested visitors to participate in citizen science activities in the park and at home—other more targeted communication methods are more effective. Communicating with local residents about exotic and native plants might involve giving talks at garden clubs. Recruiting for citizen science might involve attention-getting posters, instructional and inspirational videos, and social media posts with updates on research. Different audiences are interested in different aspects of science and turn to different media for information. Scientists and/or communication professionals (ideally both, working together) need to define their audiences, desired outcomes, and select engagement practices accordingly. The collaboration is important, as NPS staff and academic scientists may have different connections, knowledge, and skills to reach different audiences in different ways.

Audiences may want to do science more than listen to people explain science: Teachers who brought their classes to Indiana Dunes specifically pointed this out on evaluation forms when recommending a smaller ratio of lecturing to field work. And the scientists realized afterward that they needed more advice from RLC staff on actively engaging the public in the field and refining their communication skills. All professional participants in that case—communications experts, scientists, and teachers—have a role to play in fostering active, hands-on learning in parks.

Doing science rather than hearing about it takes more time but the interests and rewards are great. The DMP leaders soon discovered that sampling events often continued past the published ending time. Students were reluctant to stop searching for invertebrates; parents and teachers asked scientists follow-up questions about what happens with samples sent to USGS laboratories, about mercury, and about food webs. As one teacher helped a student use calipers to measure larvae, other students observed dragonfly feeding behaviors and pressed the teacher for information on food webs. This teacher called it "One of the best teaching days of my life." Observing, developing questions out of natural curiosity, and testing concepts about how the world works are the foundation of the scientific enterprise—and these students genuinely experienced it through a project that sent them into the water to look closely at a new ecosystem, and with a teacher who was ready to provide answers and seed new questions.

Audiences like insight into scientists as real people: Biologists who tell stories about their research reveal not only the methods, results, and significance of their work; they also reveal themselves as interested, animated, passionate human beings who do exciting things. Teachers at the Changing Tides workshop said their students would love to Skype the bear biologists and follow their projects on social media—that is, to establish relationships with them, see what their lives are like, and understand who they are and what motivates them. Students at the Indiana Dunes events were asked in advance to describe character traits of scientists; Curious, Intelligent, Inquisitive, and Observant were among the most-used terms. Scientists at the event talked in person about how they embody those characteristics.

Communication may take a lot of work: The Second Century Stewardship initiative requires all fellows to budget for at least 80 h of communication work (in addition to a 3-day communication workshop) during their 1- or 2-year fellowships. Many applicants are initially surprised by that requirement, but once in the program, realize that it is an underestimate—recording, editing, and producing videos, or polishing a good talk or popular article, or keeping up with social media all takes time. It is important that researchers recognize this and budget accordingly at the beginning of projects, especially those with goals like improving management or education.

The impacts of science communication and public engagement with science in parks need rigorous study: As we previously noted, research on informal science learning in national parks is generally missing from an otherwise vast literature. Typically, we measure outputs—like how many interpreters have viewed videos about climate change science in the course of their training—or gain some feedback on what participants get out of an outreach event. There is little rigorous evaluation of outcomes like changing participants' understanding of science, attitudes about science, desire to learn more science, etc. As a federal agency, the NPS has reduced leeway to survey the public and assess such outcomes. Academic researchers (including social scientists who could collaborate with natural scientists in studying the efficacy of science communication and public engagement) have more leeway to study outcomes. This is a rich and untapped area of cross-disciplinary research.

Conclusion and prospects

Over the past 100 years, interpreters, educators, and other communicators in the NPS have become experts at informing visitors about the unique resources (e.g., the world's tallest trees) found in national parks. They have consistently mastered and applied the art of explaining the significance of resources, helping visitors find personal meaning in them, and inspiring people to care about these protected places (Larsen 2011). Communicating the science through which we understand these unique places and resources, however, is a relatively new role. It is one that the NPS is increasingly embracing and refining. Interpreters and other communicators now communicate both the results and the processes of science—i.e., not just what we know about the tallest trees, but also how we know it. Relevant messages include: How is science done? How do scientists connect evidence to conclusions? How do scientists change their view of the world as a result of doing research? What do scientists not know, and what do they debate? What value do visitors place on science in their lives?

Interpreters engage visitors in these and other ideas through audience-centered techniques that are similar to what some faculty use in classrooms. They tell stories about scientists to convey the content, excitement, and meaning of science. They collaborate on citizen science and other forms of participatory learning. They prompt visitors through dialog to wonder, explore, and pose their own questions about data, graphs, and models. Like many faculty, interpreters are transitioning from "the sage on the stage to the guide on the side." Given this change in interpretation, scientists have endless opportunities to share their experience and collaborate with the NPS in developing, testing, and refining science communication and engagement in parks. The "Science as a Way of Knowing" initiative of the SICB (Moore 1984) highlights integrative and comparative biologists' innovative thinking about science education. Although it is 35 years old, it offers timeless ideas and common language that enable biologists and interpreters to tap the science education potential of national parks for the next 100 years.

We close with a question that is implicit to our essay: why is science worth understanding and experiencing? Apart from the economic and democratic reasons we alluded to at the start, there is at least one humanistic reason and it has much in common with national parks. Charles Darwin expressed it when he concluded *The Origin of Species* with an ode to science:

> There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

We think all integrative and comparative biologists would agree that this view of life does contain grandeur, and likely even more. Dawkins (2003) extended Darwin's idea: "There is more than just grandeur in this view of life … . There is deep refreshment to be had from standing up full-face into the keen wind of understanding (p. 13)." Furthermore, "The real world, properly understood in the scientific way, is deeply beautiful and unfailingly interesting. It's worth putting in some honest effort to understand it properly, undistracted by false wonder and prostituted pseudoscience (p. 43)." These words—grandeur, beautiful, wonderful—point to aesthetic and emotional values of scientific experience outside the practical value of scientific knowledge. Those emotional values invite and reward the intellectual pursuit of science and we suspect they have accompanied and sustained every scientist's educational and professional life in science. They are worth sharing.

National parks offer everyone the chance to experience the unique grandeur, beauty, and wonder of natural features like Yosemite Valley and to connect with shared human experience in cultural landscapes like Gettysburg or Ellis Island. Surely they offer as well the chance to experience the grandeur, beauty, wonder, and human experience of science. The future is bright as more and more scientists come to parks and collaborate with NPS staff to make their science part of the visitors' experience.

Acknowledgments

We thank M. Byappanahalli, M. Nevers, J. Pfeiffenberger, D. Shelley, W. Smith, and S. Thurston for invaluable information about their science outreach and engagement examples in parks. We thank M. Storksdieck, J. Thompson, M. Stern, and J. Dennis for helpful discussions and suggestions about the manuscript, including references to published literature. We thank several anonymous reviewers for their comments that greatly improved this manuscript. The views in this article are those of the authors and not necessarily of the NPS.

Funding

This work was supported by the National Park Service, the US Geological Survey-NPS Water Quality Partnership, and the University of Maine.

References

Beard CA, Thompson JL. 2012. Engaging visitors in climate change communication: a case study of southern Florida's national parks and wildlife refuges. Appl Environ Educ Commun 11:25–34.

Bell L, Lowenthal C, Sittenfeld D, Todd K, Pfeifle S, Kollmann EK. 2017. Public engagement with science: a guide to creating conversations among publics and scientists for mutual learning and societal decision-making. Boston: Museum of Science.

Dawkins R. 2003. A devil's chaplain. Boston: Mariner Books.

Eagles-Smith CA, Ackerman JT, Willacker JJ, Tate MT, Lutz MA, Fleck JA, Stewart AR, Wiener JG, Evers DC, Lepak

JM, et al. 2016. Spatial and temporal patterns of mercury concentrations in freshwater fish across the Western United States and Canada. Sci Total Environ 568:1171–84.

Falk JH, Dierking LD. 2010. The 95 percent solution. Am Sci 98:486–93.

Fenichel M, Schweingruber HA. 2010. Surrounded by science: learning science in informal environments. Board on science education, Center for Education, Division of Behavioral and Social Sciences and Education. Washington, DC: The National Academies Press.

Flanagan Pritz C, Nelson SJ. 2017. Collecting data on Charismatic Mini-Fauna: public participation and the dragonfly mercury project. Maine Policy Rev 26:50–4.

Larsen DL. 2011. Meaningful interpretation: how to connect hearts and minds to places, objects, and other resources. 2nd ed. Fort Washington: Eastern National.

Moore JA. 1984. Science as a way of knowing—evolutionary biology. Am Zool 24:467–534.

National Academies of Sciences, Engineering, and Medicine. 2017. Communicating science effectively: a research agenda. Washington, DC: The National Academies Press.

National Park Service. 2006. Management policies 2006. Washington, DC: National Park Service.

National Research Council. 2009. Learning science in informal environments: people, places, and pursuits. In: Bell P, Lewenstein B, Shouse AW, Feder MA, editors. Committee on learning science in informal environments. Board on Science Education, Center for Education, Division of Behavioral and Social Sciences and Education. Washington (DC): The National Academies Press.

Nelson SJ, Webber HM, Flanagan Pritz CM. 2015. Citizen scientists study mercury in dragonfly larvae: dragonfly larvae provide baseline data to evaluate mercury in parks nationwide. Natural Resource Report Series NPS/NRSS/ARD/NRR—2015/938. Fort Collins, CO: National Park Service.

Packer J. 2006. Learning for fun: the unique contribution of educational leisure experiences. Curator 49:329–44.

Pew Research Center. 2015. Beyond distrust: how Americans view their government. Washington DC: Pew Research Center.

Rogoff B, Callanan M, Gutierrez KD, Erickson F. 2016. The organization of informal learning. Rev Res Educ 40:356–401.

Sauvajot RM. 2016. Science for our National Parks' second century: a view from the top. Ecosphere 7:e01607.

Schwan S, Grajal A, Lewalter D. 2014. Understanding and engagement in places of science experience: science museums, science centers, zoos, and aquariums. Educ Psychol 49:70–85.

Shirk, JL, Ballard HL, Wilderman CC, Phillips T, Wiggins A, Jordan R, McCallie E, Minarchek, M, Lewenstein BV, Krasny ME, et al. 2012. Public participation in scientific research: a framework for deliberate design. Ecology and Society 17:29.

Stern MJ, Powell RB. 2013. What leads to better visitor outcomes in live interpretation? J Interpret Res 18:9–43.

Stern MJ, Powell RB, Cook C. 2010. The benefits of live interpretive programs to Great Smoky Mountains National Park. Park Sci 27:62–6.

Storksdieck M, Stylinski C, Bailey D. 2016. Typology for public engagement with science: a conceptual framework for public engagement involving scientists. Corvallis, OR: Center for Research on Lifelong STEM Learning.

Thompson J, Davis S, Mullen K. 2013. Climate change communication campaign planning: using audience research to inform design. George Wright Forum 30:182–9.

Zoellick B, Nelson S, Schauffler M. 2012. Participatory science and participatory education: bringing both views into focus. Front Ecol Environ 10:310–3.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 77–84
doi:10.1093/icb/icy026
Society for Integrative and Comparative Biology

SYMPOSIUM

Beyond the Brown Bag: Designing Effective Professional Development for Informal Educators

Louise Allen,[1,*] Cynthia Char,[†] Nickolay Hristov,[‡] Tracey Wright[§] and Martha Merson[§]

*Department of Biology, Winston-Salem State University, 601 S. Martin Luther King Jr. Drive, Winston-Salem, NC 27110, USA; [†]Char Associates, Montpelier, VT 05602, USA; [‡]Center for Design Innovation, 450 Design Avenue, Winston-Salem, NC 27101, USA; [§]TERC, The Education Research Collaborative (ERC), 2067 Massachusetts Ave, Cambridge, MA 02140, USA

From the symposium "Science in the Public Eye: Leveraging Partnerships" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1]E-mail: allenl@wssu.edu

Synopsis Most researchers are keenly interested in disseminating their work beyond traditional publication routes. With an eye to increasing broader impacts, scientists can benefit from partnerships with informal educators who interact daily with the public and see their role as translating science to increase the public's intellectual and emotional connections with the natural world. Typically, researchers give a one-time lunch hour talk, generally a modified version of a presentation aimed at scientific peers. Talks during which scientists show slides and interpreters mainly listen are a missed opportunity. They leave the scientist no wiser about the public's interests and the nagging questions interpreters have. Such talks leave the conscientious park educator with insufficient resources for overcoming challenges in interpreting the science for the public. The Interpreters and Scientists Working on Our Parks (iSWOOP) project proposes a model of professional development (PD) that involves a deliberate partnership where scientists and educators work together. During site-based PD sessions, they tease out the relevance to public audiences and begin to develop programs about the science. This article describes iSWOOP's approach to supporting productive collaborations that promote an understanding of scientific research to public audiences. Results from a pair of surveys indicate that both sides of this partnership benefit from extended contact and clear communication.

Introduction

National parks are our nation's "laboratories" for scientific research. This nearly invisible function is driving us to learn how to help National Park Service (NPS) interpreters move science from static facts to a lively exchange based on scientists' current, park-based research.

The Interpreters and Scientists Working on Our Parks (iSWOOP) model brings together dedicated scientists, passionate NPS rangers, and talented STEM education researchers who are committed to expanding STEM learning opportunities at our nation's parks (Fig. 1). The project has the potential to transform the way the NPS Division of Interpretation and Education leverages site-based science, the way its education rangers (hereafter called interpreters) communicate site-based science to the public, and expands opportunities for scientists to make their efforts visible to the public. Interpreters may be experts at interpretation, but not on the particular science they are communicating. In the mid-2000s, Hristov and Allen noticed the missed opportunities to highlight cutting-edge science about the Brazilian free-tailed bats. Without exposure to scientists, interpreters relied on ranger lore and Internet searches, which sometimes resulted in dated information or facts true of other species, but not the free-tails that the public gathered to watch. This has been ongoing, ever-present conundrum with a variety of proposed solutions (Macdonald 2013; Melena 2015).

Interpreters have a pressing need for first-hand knowledge of site-based research initiatives (Char 2015). However, the typical format for briefing park staff about research is a one-time lunchtime research

Advance Access publication May 31, 2018

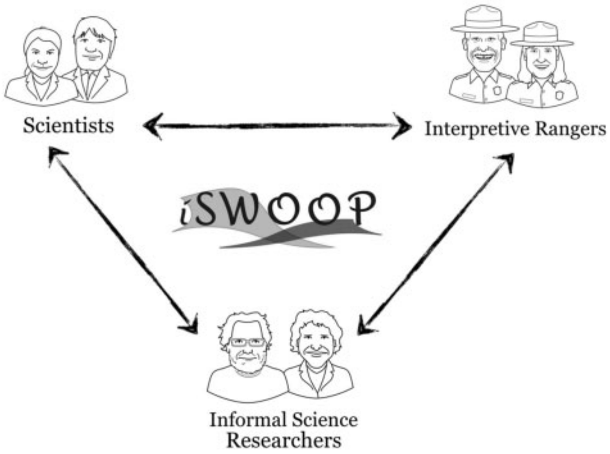


Fig. 1 The iSWOOP model includes bidirectional exchange of benefits and input from three partners; Scientists, informal STEM learning researchers, and national park rangers. Ultimately it is the public, specifically visitors to these national parks that benefit from these purposeful interactions.

talk to a group of rangers, with little opportunity for two-way conversations or hands-on experience. iSWOOP affords new structures to foster interactions among scientists and interpreters. The public regards interpreters as trusted sources for information, even on sensitive topics like climate change (Pew Research Center 2015). When confident, knowledgeable, and equipped with a repertoire of strategies, interpreters have the potential to engage tens, and ultimately hundreds of thousands of park visitors in learning about park-based science, multiplying the broader impact of the collaborating scientists well beyond what they might achieve themselves (Merson et al. 2017).

Scientists are ideal partners in developing interpreter skill sets and knowledge around the science they are tasked with communicating. Scientists are in a position to make a difference, but how do they make a difference, particularly in a complex bureaucratic system that features high levels of staff turnover? Here, we describe the iSWOOP model of professional development (PD). We ask: What aspects of iSWOOP's PD model are valued by interpreters and scientists? We regard effective PD as the precursor to changes in practice that allow meaningful opportunities for the public to become aware of park-based research. We posit that effective PD requires effort and time to allow interpreters to explore the body of research and then to create meaningful opportunities for the public while in dialog with the scientist.

The iSWOOP model

iSWOOP adopted activities and approaches used extensively in inquiry-oriented PD workshops for informal educators in zoos and science centers (see Building Math Momentum in Science Centers, NSF Award No. 0229782, https://nsf.gov/awardsearch/showAward? AWD_ID=0229782). We piloted iSWOOP PD at Carlsbad Caverns and refined the model, adapting as needed to meet circumstances at new park units across the country. The structure of the model includes multiple touch points, modeling, and opportunities to do science. Practitioners' questions shape the agenda. An emphasis on visualization dovetails with interpreters' mission: to reveal the resource and make meaningful connections with significant cultural and natural resources (Tilden 1957; Ham 2013). In this case, scientists and interpreters tease out the story of the researcher, previous lines of work, and explore the relevance of the research within and beyond park boundaries (Firestein 2012).

Interpreters and researchers convene for multi-hour sessions over 3–5 days. The sessions begin with listing questions about the natural resource (Table 1). Interpreters list questions that nag at them, and also those that visitors ask repeatedly or are otherwise memorable. The questions shape subsequent sessions. Scientists demo their high- and low-tech instruments to explain how we know what we know. A block of time is also dedicated to hands-on experience. Interpreters assist with data collection, gaining firsthand experience with the tools, frustrations, and workflow. The sessions include an overview of the visualizations scientists use to make sense of their data, e.g., graphs, 3-D models, contrasting slides of the phenomenon under different conditions, and animations. Interpreters craft a program. They imagine a setting for their interactions with the public, a hook, and open-ended questions to encourage observation, prediction, and speculation. The PD culminates with a run-through of new programs during which all participants offer feedback, clarify scientific points, and suggest ways to heighten engagement, suspense, and curiosity.

Given the intensity of the commitment, we set out to determine the extent to which this investment pays dividends for both scientists and interpreters. Both iSWOOP evaluators' studies and the literature on PD speak to the benefits of a multi-session model that prioritizes exchange, first-hand experiential learning, modeling of interpretive techniques, as well as new content.

Research underpinning the iSWOOP approach

From the outset, iSWOOP relied on interpreters as well-positioned intermediaries for STEM learning.

Table 1. Subset of questions posed by interpreters from three national parks on the first day of iSWOOP professional development training sessions

Area of expertise of collaborating scientist(s)		
Bat behavior and ecology	**Ecology of Joshua trees**	**Landscape change and glaciation**
• How many bats are in the cave? • How fast do bats fly? • Do they stay in a group and/or run into each other? • Where/how far do they go in search of food? • How do females know their pup from others? • How does the size of a bat alter the thermal reading?	• How old are the Joshua trees? • I heard the Joshua trees are dying. What are you doing about it? • Why do they only grow here? • Is the only way for the Joshua tree to reproduce through pollination by the Yucca moth? • Why are there no Joshua trees in this part of the park? • How is climate change affecting Joshua trees?	• How are the islands changing? • How many forest fires have there been? • What species are here in the park now versus in the past? • Why is flowering in this area delayed 2 weeks compared with others? • How long does it take the coastline to erode? • Why are some coastlines higher than others?

The literature on interpretive aims speaks to their strengths as credible conduits for scientists' work (Tilden 1957; Ham 2013). To inform the iSWOOP model, we also surveyed available literature about effective PD designed to build educators' content knowledge and increase their use of inquiry-based approaches to STEM topics. Three themes stood out related to bolstering educators' ability to facilitate STEM learning: (1) the importance of authentic practice of science, (2) the need includes but is not limited to new content, and (3) effective PD takes time. By "practice" we mean shadowing scientists as they work or independently engaging in designing experiments, refining questions, and conducting fieldwork or analysis. We specify "authentic" to indicate that the activities contribute to research and are not solely for the sake of demonstration. In most PD, acquiring new understandings and participating in authentic practice overlap. For example: Falk and Drayton (2006) found that teachers' increased self-perceptions of their own scientific understanding resulted, at least in part, from their authentic practice of science during a year of research with ecologists (1997). Nevertheless, we discuss these themes separately.

(1) Authentic science practice

To provide meaningful science experiences for students, educators need quality science experiences themselves from which to draw. Researchers emphasize the importance of educators engaging in science investigations and experiencing the same approaches that they will adopt with learners (Rosebery and Warren 1998; Bevan and Xanthoudaki 2008). PD sets precedents for participants to draw less upon the traditional techniques associated with K-12 rote learning and more on inquiry-based techniques appropriate to fostering learning in an informal setting. In their comparison of three workshop models with a museum component, Melber and Cox-Petersen (2005) found teachers participating in the model which combined museum and field-based activities gave it the highest mean rankings. Teachers who participated in workshops with a field component reported specific elements that helped them understand the process of science.

(2) Limitations of new content

The need for PD includes but is not limited to new content (Tran and King 2007). Several studies have found that content coverage may lead to improved confidence without corresponding increase in competence (Sukow 1990; Smith et al. 1998). In a study of 376 programs in 24 units of the US NPS, interpreter confidence was associated with visitor satisfaction and lack of confidence with visitor attrition. However, the walking encyclopedia approach was also associated with visitor attrition (Stern and Powell 2013).

Because their audience members may not want to think hard about complex numerical information (Bruine de Bruin et al. 2017), equipping interpreters with only facts, statistics, or numerically expressed relationships may cause visitors to turn-off. Some audiences will focus on qualitative communication more than on quantitative communication (Canfield et al. 2017). This makes the interpreters' job of revealing the significance of a resource to the public particularly challenging (Tilden 1957; Ham 2013). The antidote? Scientists' ways of looking at resources can provide revelations about structure, function, and dynamic interactions that can be communicated qualitatively. Effective PD assists interpreters in integrating new knowledge and delivering it with appropriate techniques including stories, props, quotes, and images. Ideally, techniques increase engagement, visitors' appreciation of the relevance of research, and make the material memorable. While content knowledge is a component of successful interpretation, it must be tempered with an assessment of audience members' interest and likely saturation point.

(3) Time commitment

Effective PD takes time and a sustained effort (Yoon et al. 2007; Loucks-Horsley et al. 2010). Studies of PD find that one-time interventions are less likely to shift practice than when educators have multiple opportunities to encounter new content, to meet with peers, and to engage in discussion and practice in adopting new content and approaches (Garet et al. 2001; Melber and Cox-Petersen 2005). An example: nature center staff who participated in PD programs where they were provided with resources to work on the topic over time were more likely than staff at non-participating centers to be comfortable with and provide climate change education programming (Swim et al. 2017).

When scientists and interpreters have the opportunity to meet and work collaboratively the outcomes are impressive. For example, the NASA-NPS Earth to Sky Partnership's science and communication courses feature NASA scientists as presenters who are coached by experienced interpreters, and who participate in class discussions. Evaluators tracking three cohorts of participants over the course of 2 years determined that over 4 million National Park and Wildlife Refuge visitors were reached by participants with content derived from the courses, and that they provided training on course content to over 2,000 additional educators (https://www.earthtosky.org/professional-development/effective-training.html). Halversen and Tran's COSIA project (2010) gives an entire semester to fostering collaborations among ocean scientists and informal educators to foster students' science communication skills.

With these considerations in mind, iSWOOP project leaders designed a PD model for National Park Interpretive rangers that is based on: (1) participation in authentic science practices, (2) direct contact with time for exchange of stories, questions, and information, and (3) science content conveyed with relevance and that models interactive techniques.

Overview of two studies

Using a mixed methods approach which collects and analyzes both qualitative and quantitative data (Creswell and Plano Clark 2007), the project evaluator and principal investigators have been studying the project's PD at three national park units located in the southwest, northeast, and midwest. In each park site, between 8 and 15 interpreters attended PD sessions along with interested others (such as administrators, communications staff, and resource managers). The groups gathered for roughly 15 contact hours spanning several days. Scientists' attendance ranged from 3–15 h. Data were gathered following PD through a survey for interpreters (Study 1) and a survey for scientists (Study 2).

Quantitative data yielded from rating scales were analyzed using frequency distributions and descriptive statistics. Prose responses to open-ended questions were coded by a member of the evaluation team, using a grounded theory approach (Patton 2002; Charmaz 2006) using thematic categories in alignment with the main features and goals of the project.

Study 1: Interpreters' feedback on iSWOOP PD

Methods and sample

On the last day of training, participants from three National Park sites ($n = 37$) completed an anonymous 15-item survey designed to gauge their impressions of the relevance of skills and content covered. Interpreters rated the value of PD components and made recommendations for future sessions.

Results

Overall, interpreters greatly appreciated the training's featuring of scientists and park-based research. They embraced the idea of engaging visitors in conversations about park-based scientific research. As one interpreter commented on the applicability of iSWOOP's PD:

> The concept of this project is great. I think we often aspire to interpret current research, but often fall back on more general information and/or synthesize research for visitors. The focus on actually engaging visitors with the data has great potential both for making current science more accessible to the visitor and in contributing to helping the public to become more scientifically literate.

Participants' feedback underscored the value of the PD in terms of (1) increasing their grasp of park-based scientific research, (2) strengthening relationships with featured scientists, and (3) acquiring the skills to make conversations about research interactive. The training prepared interpreters to speak confidently about park-based research.

> I thought this was valuable professional development, especially in the life of interpreters. There's always a disconnect between scientists/academic way of speaking and (my) tendency to "over-simplify" research. iSWOOP is a means by which we can truly meet visitors on their level.

Over half (20 interpreters, 54%) of interpreters cited their classroom-based and field-work with the scientists as the most valuable aspect of the PD. Interpreters reported that the training content strengthened both their knowledge and skills. Twenty-nine (29) out of 37 interpreters (78%) agreed that training had given them new knowledge to apply in their work. Nearly, two-thirds (23 interpreters; 62%) agreed that the training had given them new ways to look at their interactions with visitors. Over half (20 interpreters, 54%) agreed that iSWOOP PD had increased their skill facilitating discussions of visualizations, research, and relevance of scientific research to visitors' lives. Similarly, they felt equipped to tell stories about how scientists know what they know.

Interpreters expressed a desire for continued communication with the featured researchers. Among the recommendations were requests for more—contact with more researchers, over longer periods of time, and with more opportunity for informal exchanges. Almost half (17 interpreters, 46%) identified maintaining a connection with scientists and updates on the research as the primary request for ongoing support.

Study 2: Scientists' perspectives

Methods and sample

Evaluators sent a survey to the research scientists who had shared their research during PD sessions. All but one of the eight surveyed also contributed material to the visual library and met multiple times with project leaders. The 8-item survey addressed the reasons scientists might choose to become involved, the potential professional benefits and outcomes of the project, and suggestions of how the project model could be improved. Surveys were administered after PD sessions had occurred.

Eight of the nine research scientists involved in the iSWOOP during the first 2 years of the project completed a survey. The scientists represented five different universities and a variety of scientific departments (e.g., biology, geology, paleoecology, and earth/climate sciences) and included two assistant professors, two associate professors, three retired (emeritus) professors, and one *post doc* researcher.

Results

Scientists were enthusiastic about the potential benefits. Their comments ranged from personal gain to following through on a commitment to a larger societal benefit

> To me, it seemed like a win-win—I get to get my message out there, and the park gets to tell stories about the "what" and "how" of science. It's also important for people to know that parks aren't just beautiful or fun; they're also important natural resources, and a lot of research is happening in them . . .

Seven of the eight scientists indicated that they had gained something professionally valuable from the project. Benefits described by the scientists were varied, and included: an increased professional network of colleagues, improved communication skills, a deeper understanding of working with parks and park interpreters, and greater appreciation of visitor perspectives and the importance of out-of-school learning.

At least half (four to five out of eight) of the scientists identified four different areas in which they reported the project had impacted them either "moderately" or "extremely." These areas were: (1) broadening their impact by reaching new or larger audiences for their work; (2) adding to their repertoire of teaching strategies; (3) increasing the ways they will work with NPS or interpreters in the future, and (4) changing how they see visitors' or interpreters' perspectives on their work.

The main project feedback offered by the scientists suggested greater attention to three areas: identify ways to minimize the time commitment, improve project communication between the various project partners, and explore different ways in which they could get greater credit or recognition for their involvement and contributions to the program.

Discussion

The results show that iSWOOP PD delivered welcome benefits to its participants. For interpreters, benefits were tied to accomplishing their job. For scientists, the benefits were varied. Expanding their repertoire of strategies for explaining their research or gaining additional visuals to illustrate their work were mentioned along with the opportunity to contribute to a community beyond their students and institutions.

Overall, interpreters greatly appreciated contact with scientists, and the idea of actively engaging visitors in data from active scientific research.

Interpreters expressed a desire for more continued communication with the featured researchers. Attesting to this point—among the recommendations were requests for more, e.g., more researchers, more contact over longer periods of time, and more informal exchanges were desirable. This however sets up a fundamental conflict between key participants (e.g., interpreters wanting more time and scientists wanting to commit less time). In order to address these tensions, we have advocated for increased "soft" collaborative time, including spending time together at meals during the span of PD and for continued communication in a way that is respectful of the scientists' time (e.g., many scientists have twitter handles that the interpreters can keep up with and communicate with while also moving the conversation to the public realm).

iSWOOP has not solved all of the challenges associated with science communication happening in parks. Interpreters and scientists recognize the challenges: visitors with a wide range of ages, science interest and understanding, and motivation for their visits. Intergenerational groups on vacation with a specific recreational goal can be a challenge to talk to at length about current research. In asking for more researchers and more contact with researchers, interpreters conveyed their need to meet visitor interests, to leverage place-based interest, and the depth of knowledge needed to manage these dynamics in formal and informal interactions. In the face of these challenges, iSWOOP PD appears to increase interpreter content knowledge, and provides visualizations and stories which can be used to hook audiences, maintain their interest, and forge connections.

Models for PD of this sort also need to consider managing both logistics and varied expectations. For example, expectations and benefits need to be clear and realistic. It is helpful to agree upfront on whether everyone who participates in PD will also be expected to interpret the science. Will interpreters have access to scientists or other supports as they refine their programs and introduce the featured scientists' content? How will scientists' contributions be credited in ways that are meaningful to them?

The iSWOOP project takes as a given that individuals may enjoy the PD and will have constructive criticism, but find reasons not to adopt the approaches. Interpreters have offered numerous suggestions for improving the PD. Meeting their needs is a high priority, yet the needs are varied for new and seasoned interpreters and those whose style is more factual versus conversational or narrative-driven. Even with park-specific, job-, and park-relevant PD, some participants will find reasons not to adopt the content or strategies covered in iSWOOP PD. Hord et al. (2006) delineate seven kinds of concerns (Stages of Concern or SoC) that users, or potential users, of an innovation may have in their concerns based adoption model (Table 2). It is ultimately up to interpreters' supervisors to shepherd the adoption process. However, the project has tried to anticipate concerns and proactively plan PD activities to address them, such as practice sessions with feedback from PD leaders and featured scientists.

There are several limitations of these studies. The process for structuring PD is still being refined and implementation at different parks is not identical. Respondents did not have an equal stake in the project or its outcome. For example, one of the scientists had been involved peripherally and two of the scientists had joined the project as consultants on visuals rather than in the role of featured scientist. Some PD attendees were expected to develop formal programs based on iSWOOP training while others had the option to use iSWOOP approaches or not.

However, given that effective PD prioritizes (1) doing science together, (2) increasing interpreters' science content and first-hand experience with science process, (3) time for exchanges that meaningfully benefit interpreters and scientists, iSWOOP evaluators and researchers continue to collect data so that those aiming to implement iSWOOP approaches can address interpreters' and scientists' needs.

Conclusion

A common format for exchanges between interpreters and scientists involves a researcher giving a one-time talk, generally an adaptation of a presentation for peers or students. The scientist may speak with the implicit hope that certain findings will be disseminated to the public. These talks can highlight scientists' findings, however, this format tends to fall short of providing the material interpreters need to forge emotional and intellectual connections with visitors (Tilden 1957; Ham 2013). To increase the public's awareness of park-based research, interpreters need background on studies, stories about the researchers, props or visuals to explain methods and challenges, and a plethora of ideas, metaphors, or analogies for establishing relevance. Without meaningful time for exchanges with interpreters, scientists miss out on opportunities to hear interpreters' questions and observations formed as a result of daily observations of the resources. New models are needed which prioritize an exchange.

Table 2. Seven stages of concern from Hord et al. (2006) with potential stage specific expressions from the iSWOOP project

Stages of concern	Expression of stage of concern from iSWOOP interpreters
6. Refocusing	I'd like to try with … laminated photos, … with an iPad, … a different topic, etc.
5. Collaboration	What do scientists expect?
4. Consequence	Will visitors be interested?
3. Management	Can I manage the technology? Is there time to prepare? When and where to begin?
2. Personal	What do I have to give up (that I like or am good at)? How might using iSWOOP approaches affect me and my feelings of competence?
1. Informational	Do I understand the visuals? Do I have sufficient material to tell a story about the researchers?
0. Awareness	I am not involved because I focus on history or questions about basic needs only.

Interpreters are well-acquainted with the questions to which the public craves answers. The iSWOOP project is testing its model of PD that starts with interpreters' and visitors' questions, structures direct contact for interpreters and scientists during fieldwork and seminar-style interactions, and affords time together for meaning making.

Science communication is of vital importance because it seeks to inform decision making, but science is nuanced and complicated (Fischhoff 2013). Uncertainty is implicit in science, and grappling with this takes time and skill. The iSWOOP model allows scientists a powerful way to connect with the public via an extensive network of trustworthy informal educators in the National Parks System (Merson et al. Forthcoming 2018, this volume), eager to tell the story. We have provided interested readers with a Sample PD Outline and a Planning Worksheet to help them better connect with informal science educators (see Supplementary Material).

Acknowledgments

We thank park interpretive, education, resources and management staff from Acadia, Carlsbad Caverns, Indiana Dunes, and Joshua Tree, and NPS leadership and our advisory board members.

Funding

The iSWOOP project was made possible with support from the National Science Foundation DRL-123030 and DRL-1514776. The symposium, Science in the Public Eye: Leveraging Partnerships, was made possible with support from the National Science Foundation DRL-123030 as a part of the iSWOOP project. The following divisions of the Society of Integrative and Comparative Biology have generously supported the symposium: Division of Animal Behavior, Division of Comparative Biomechanics, Division of Comparative Endocrinology, Division of Ecoimmunology and Disease Ecology, DNB (Division of Neurobiology), and Division of Vertebrate Morphology. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the view of the National Science Foundation or the Society of Integrative and Comparative Biology.

Supplementary data

Supplementary data are available at *ICB* online.

References

Bevan B, Xanthoudaki M. 2008. Professional development for museum educators: unpinning the underpinnings. J Mus Educ 33:107.

Bruine de Bruin W, Wallin A, Parker AM, Strough J, Hanmer J. 2017. Effects of anti- versus pro-vaccine narratives on responses by recipients varying in numeracy: a cross-sectional survey-based experiment. Med Decis Making 37:860–70 (https://doi.org/10.1177/0272989X17704858).

Canfield C, Bruine de Bruin W, Wong-Parodi G. 2017. Perceptions of electricity-use communications: effects of information, format, and individual differences. J Risk Res 20:1132–53 (https://doi.org/10.1080/13669877.2015.1121909).

Char C. 2015. To be more inquisitive in the natural world: evaluation of the Interpreters and Scientists Working on Our Parks (iSWOOP) (http://iswoopcave.com/? page_id=32).

Charmaz K. 2006. Constructing grounded theory. Thousand Oaks (CA). Sage Publications.

Creswell JW, Plano Clark V. 2007. Designing and conducting mixed methods research. Thousand Oaks (CA). Sage Publications.

Falk J, Drayton B. 2006. Dimensions that shape teacher–scientist collaborations for teacher enhancement. Sci Teacher Educ 90:734–61.

Firestein S. 2012. Ignorance How it Drives Science. New York (NY): Oxford University Press.

Fischhoff B. 2013. The sciences of science communication. Proc Natl Acad Sci U S A 110:14033–9.

Garet MS, Porter AC, Desimone L, Birman BF, Yoon KS. 2001. What makes teacher development effective? Results from a national sample. Am Educ Rev J 38:915–45.

Halversen C, Tran LU. 2010. Communicating ocean sciences to informal audiences: a scientist–educator partnership to prepare the next generation of scientists. New Educ 6:265–79.

Ham SH. 2013. Interpretation: making a difference on purpose. Golden (CO): Fulcrum Publishing.

Hord SM, Rutherford WL, Huling L, Hall GE. 2006. Taking charge of change. Austin, TX: SEDL.

Loucks-Horsley S, Stiles KE, Mundry S, Love N, Hewson PW. 2010. Designing professional development for teachers of science and mathematics. Thousand Oaks (CA): Corwin.

Macdonald B. 2013. Interpreting conservation: communicating about natural resources, scientific research, and critical environmental issues at Cape Cod National Seashore [thesis]. [Amherst (MA)]: University of Massachusetts.

Melber LM, Cox-Petersen AM. 2005. Teacher professional development and informal learning environments: investigating partnerships and possibilities. J Sci Teach Educ 16:103–20.

Melena S. 2015. Conversation guide for park teams—collaboration for resource stewardship and relevance [draft 3]. Fort Collins (CO): National Council for Interpretation, Education, and Volunteers, Relevance and Inclusion Natural Resource Stewardship and Science, Office of Education and Outreach Interpretive Development Program.

Merson M, Hristov N, Allen L. Forthcoming 2018. Science in the public eye: leveraging partnerships an introduction. Integr Comp Biol (doi:10.1093/icb/icy034).

Merson M, Char C, Hristov N, Allen L. 2017. Seeking park-based science information: interpreters at the gate. George Wright Forum 34:368–80.

Patton MQ. 2002. Qualitative research and evaluation methods. 3rd ed. Thousand Oaks (CA). Sage Publications.

Pew Research Center. 2015. Ratings of federal agencies, Congress and the Supreme Court [Internet]. Washington (DC): Pew Research Center [cited December 29, 2017] (http://www.people-press.org/2015/11/23/4-ratings-of-federal-agencies-congress-and-the-supreme-court/).

Rosebery AS, Warren B. 1998. Boats, balloons and classroom video: science teaching as inquiry. Portsmouth (NH): Heinemann.

Smith WS, McLaughlin E, Tunnicliffe SD. 1998. Effect on primary level students of inservice teacher education in an informal science setting. J Sci Teach Educ 9:123.

Stern MJ, Powell RB. 2013. What leads to better visitor outcomes in live interpretation? J Interpret Res 18:9–43.

Sukow WW. 1990. Physical science workshops for teachers using interactive science exhibits. Sch Sci Math 90:42–7.

Swim J, Geiger N, Fraser J, Pletcher N. 2017. Climate change education at nature-based museums. Curator 60:101.

Tilden F. 1957. Interpreting our heritage: principles and practices for visitor services in parks, museums, and historic places. Chapel Hill (NC): University of North Carolina Press.

Tran LU, King H. 2007. The professionalization of museum educators: the case in science museums. Mus Manage Curatorship 22:131–49.

Yoon KS, Duncan T, Lee S, Scarloss B, Shapley KL. 2007. Reviewing the evidence on how teacher professional development affects student achievement. Issues and Answers, REL 2007-No. 033. Washington (DC): U.S. Department of Education, Institute of Education Sciences, National Center for Education Evaluation and Regional Assistance, Regional Educational Laboratory Southwest (http://ies.ed.gov/ncee/edlabs).

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 85–93
doi:10.1093/icb/icy008

Society for Integrative and Comparative Biology

SYMPOSIUM

So You Want to Share Your Science . . . . Connecting to the World of Informal Science Learning

Carol Lynn Alpert[1]

Strategic Projects Group, Museum of Science, One Science Park, Boston, MA 02114-1099, USA

From the symposium "Science in the Public Eye: Leveraging Partnerships" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1] E-mail: calpert@mos.org

Synopsis Scientists can reap personal rewards through collaborations with science and natural history museums, zoos, botanical gardens, aquaria, parks, and nature preserves, and, while doing so, help to advance science literacy and broaden participation in the natural sciences. Beyond volunteer opportunities, which allow scientists to contribute their knowledge and passion within the context of existing programs and activities, there are also opportunities for scientists to bring their knowledge and resources to the design and implementation of new learning experiences for visitors to these informal science learning organizations (ISLOs). Well-designed education outreach plans that leverage the expertise and broad audiences of ISLOs can also enhance the prospects of research grant proposals made to agencies such as National Science Foundation, which encourage researchers to pay careful attention to the broader impacts of their research as well as its intellectual merit. Few scientists, however, have had the opportunity to become familiar with the pedagogy and design of informal or "free-choice" science learning, and fewer still know how to go about the process of collaborating with ISLOs in developing and implementing effective programs, exhibits, and other learning experiences. This article, written by an experienced science museum professional, provides guidance for individual scientists and research groups interested in pursuing effective education outreach collaborations with science museums and other ISLOs. When prospective partners begin discussions early in the proposal development process, they increase the likelihood of successful outcomes in funding, implementation, and impact. A strategic planning worksheet is provided, along with a carefully-selected set of further resources to guide the design and planning of informal science learning experiences.

Introduction

"Have I made my case? Will our paper be accepted? Who will read it? What is the impact factor? Etc . . . ." Hold on; let us step back for a moment from the pressures of career science. Some of you may remember the days when just getting to participate in the realm of scientific discovery and exploration was a joy and a privilege; something you felt almost guilty about being paid to do, because you loved it, were inspired, and wanted to make a difference. Now you spend your days negotiating permits, following protocols, attending meetings, writing grants, advising students, and always more paperwork . . . .

There is a cure for this. It is to share your science; go back to your roots and discover ways to engage others in the wonder and fascination that first lured you into living, thinking, and doing science. First, you may need to shake off some of the seriousness of your scholarly demeanor, shed layers of technical jargon that have entwined you, lay aside your political agenda, and tunnel back to the state of wonder and joy that first got you started on this journey. (Already you are noticing the relative informality of this article, tucked within the volume's more scholarly contributions.) Now, unencumbered, what insights can you share with the not-yet-initiated: children, families, adventurers, sight-seers, students? How best can you share them? And, again, why bother? Because doing so may help you revive that lively sense of mission, curiosity, and fun that was once at the core of your own impetus for gaining insight into the scientific field that you now call your own.

I work in a science museum, and I see this happen all the time. We partner with university research centers

Advance Access publication May 24, 2018

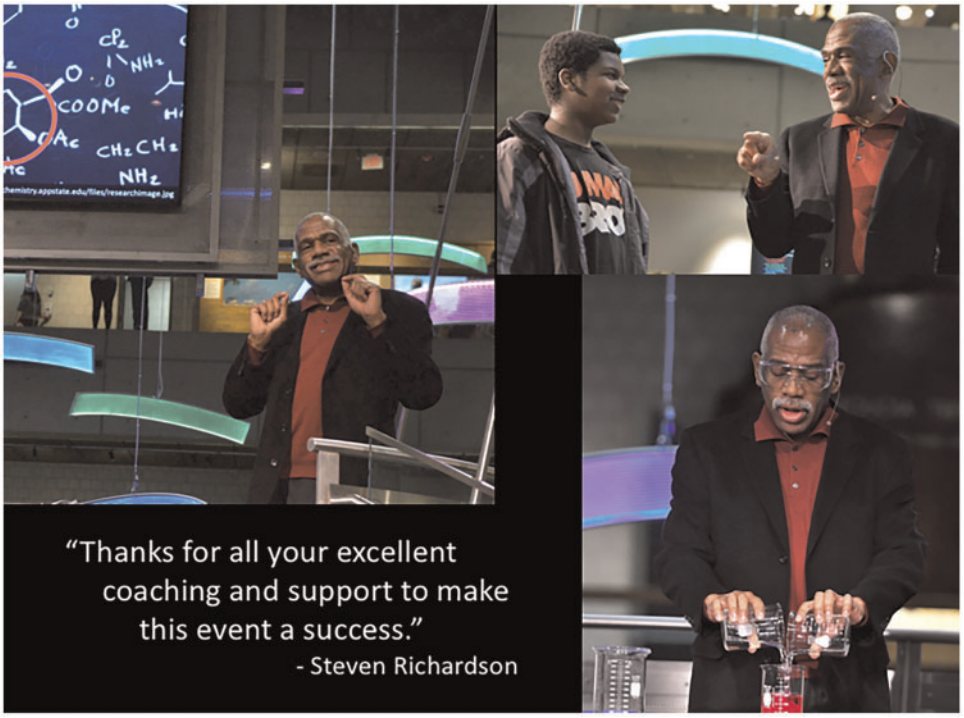


Fig. 1 Howard University Professor Steven L. Richardson shares his passion for research with Museum of Science visitors.

and labs, and we give graduate students and postdoctoral fellows opportunities to come learn how to share their science with the families, school kids, couples, and tourists who browse the spaces of our giant halls of discovery and play. We coach our scientist partners in using and designing hands-on minds-on activities related to their research, and in making short films and animations. We challenge college professors—accustomed to lecture halls and technical conference presentations—to come into our public presentation spaces and tell stories enlivened with big beautiful pictures and live hands-on demonstrations, and we workshop them through the steps of transformation from lecturer to inspirer (Fig. 1). The results can be profoundly energizing and uplifting. Here are some lightly-edited excerpts from comments we have recently captured on film from our graduate student volunteers (MOS 2017):

> In the lab you can get sort of very "in your head" about what you're working on, you're so familiar with it. And then you go and talk to people, and they're like, "wow, that's so cool!" And so, especially in graduate school, when things can be very, you know—a lot of things don't work, and you can get very sort of pessimistic and cynical—it's a lot of fun to come and talk to a much broader audience about them.
>
> When you're interacting with these children, and you just see something click, and then their face lights up, and they start explaining to you what is going on - that's really like the coolest moment ... for that moment, they're as into it as you are (Fig. 2).
>
> I think an undervalued part of our jobs as scientists is being able to advocate for what we do, and this activity of being able to reach out and connect with the general public and get them excited about science is a really important part of being able to justify the work we do.

A similar but more activist sentiment was captured in the program description of a roundtable held at the 2018 meeting of the Society for Integrative & Comparative Biology this last January: "Many students go into science not just because of the beauty of science itself, but because they want to change the world, through science communication, education, or policy" (SICB 2018). In this spirit, national organizations such as the American Association for the Advancement of Science have become more vocal in recent years, urging scientists to develop public engagement and science communication skills, especially in a political climate generally perceived as increasingly hostile to evidence-based policy-making. This article does not focus on achieving political ends; rather, it is about seizing opportunities to engage broader constituencies in the spirit of investigation, discovery, knowledge-sharing, and rational discourse embodied by science, and to assist in opening pathways for further exploration and participation.

Fig. 2 MIT Ph.D. candidate Eric Bersin delights youngsters at the Boston Museum of Science with a diamond magnetometer he and his colleagues hauled in from the lab.

Sharing science: Where to begin?

One good way to begin is to think about what audiences you or your group might want to reach, where they can be found, what they might find especially intriguing about your field, and how you might engage them by providing opportunities to see, touch, explore, ask questions, test answers, and make new connections. The agenda here is not about how much knowledge you can impart, but how deeply you can awaken in those around you those qualities of curiosity, inquiry, and enthusiasm that may prompt them to continue exploring on their own. This is the pedagogy of inquiry-based learning, and it is the hallmark of progressive classrooms and the core of the informal science learning industry—the professionals who design and provide museum programs and exhibits, citizen science and ranger interpretive programs, aquarium adventures, after-school nature clubs, and other out-of-classroom education experiences.

In fact, a good way for scientists to cultivate broader communication skills and reach a larger audience, is to get involved with these types of informal science learning organizations (ISLOs), where sharing knowledge, inquiry, and insight into the natural world is core to their mission. ISLOs are likely to host volunteer opportunities and relevant collections, plus the spaces and facilities for accommodating visitors. They are already on the map as destinations for education- and adventure-loving people; they bring in science-attentive audiences; and many of them have staff who can help researchers develop effective means of engaging visitors. So, if your time for outreach is limited, ISLOs can help you leverage your efforts.

A brief introduction to the world of informal science learning

It is considered informal because it is not required, subscribes to no one set of standards, involves no exams or degrees, and usually happens outside the classroom. Another moniker for it is “free choice learning” (Falk 2002), because participation is purely voluntary: If it is not interesting, engaging, or fun, people will simply walk out the door. So, ISLOs employ professionals skilled at designing, implementing, and evaluating these experiences to ensure that people will want to keep having them. They seem to be doing a very good job. The Association of Science-Technology Centers has over 650 members operating in 47 countries, and based on 2016 survey data, estimates 120 million annual visits worldwide and 70 million in the USA alone (ASTC 2017).

This influx of humanity is a bonanza for scientists wanting to get involved in outreach; it is far greater than the numbers who can be attracted to campus or institute venues. But their very popularity can limit the operational flexibility of larger science centers, museums, zoos, and aquaria. They are institutions with complex infrastructures. They schedule exhibits and programs, courses and visits, months and sometimes years in advance. Staff time is strictly allocated and budgets are limited. Few people realize that most US museums are not publicly-supported as are the Smithsonian Institution museums in Washington, D.C.; instead, they must make their own way on admission tickets and parking fees, grants and donations, gifts and tax breaks. This has implications that will be addressed a bit later.

The first step for the scientist is to locate potential allies and partners. Scan your community and neighboring communities; find out what organizations are engaged in providing enrichment experiences for adults and youth; read their websites, make a visit. If you are a person who works with animals, try parks, zoos, refuges, aquaria, science, and natural history museums. If you are a person who works with plants, check out botanical gardens, horticultural societies, arboretums, parks, science, and natural history museums. Do they welcome local community members? Do they attract diverse visitors? Find out if they have collections relevant to your research, inhouse scientists or curators, or educational programs that might welcome new ideas and resources. Find a person you can talk with who manages education programs, exhibit planning, or outreach; discuss the organization's needs and goals. These are the people to whom you may take your ideas, make your initial pitch—get a dose of reality perhaps—then come back with a revised approach. The reality is that they, like you, have limited bandwidth, budget, and resources, and often other very real constraints; like visitor safety, animal welfare, employment law; it is helpful to understand what some of these are. Smaller organizations can sometimes be more flexible. Perhaps your project can be slipped right into a schedule of programs being curated for next spring; perhaps there is a volunteer opportunity for someone with your talents and expertise. You may need to reimagine and reconfigure to find the best match for all concerned.

When is greater strategic collaboration required?

Sometimes, just becoming a regular volunteer is what it takes to find a satisfying outlet for your interest in sharing science with others. You may be required to go through some training and supervision to get certified to work with visitors. However, other times, it may be the case that you want to contribute something new about your work, your research, or your field; perhaps by adding a new perspective, program, or activity in addition to what is already being offered onsite. Small ISLOs may have more flexibility to do this, but also fewer resources to spare. In larger ISLOs, as in larger universities, the wheels grind more slowly. In these cases, additional consultation, planning, and development will be required; even more so if the partnership involves formal contractual arrangements, as in large research center—science museum collaborations, or if the collaboration is being written into a grant proposal as a deliverable of federal research award. While this approach requires more up-front effort, it can also help you and your colleagues realize a public engagement initiative with much greater impact than you would have been able to achieve on your own.

In fact, one big incentive for scientists to take steps toward getting involved in outreach comes in the form of guidance from science-funding organizations, who sometimes counsel applicants to include components of public outreach in their research programs. The National Science Foundation has its Broader Impacts Criterion alongside its Intellectual Merit Criterion, and this is designed to motivate applicants to use time and resources allocated from their award to address connections between research, practice, and societal impact (NSF 2018). Many NSF applicants and awardees—knowing that they do not necessarily have the confidence, skills, audiences, or venues suitable for making a significant impact on their own—look to ISLOs to help them accomplish these goals (Alpert 2009, 2013). The NSF-funded Center for the Advancement of Informal Science (CAISE) provides advice, practical tools, and encouragement. (see the Resource section further below.)

As a museum professional, I welcome the opportunity to bring scientists into the museum to interact face-to-face with our guests. Early-career researchers tend to be considerably more diverse than their more senior mentors, and we find it thrilling to see youngsters from different ethnic and cultural backgrounds light up when they get to interact with role models who look like not-much-older versions of themselves. Scientists bring authenticity to our programs, and they help us introduce state-of-the-art science and technology to our constituencies. We have learned that we need to allocate significant time and resources to cultivate these partnerships; to understand the research well-enough to help devise ways to share it, and to give the scientists and their students the training and supervised practical experience they need to feel confident and successful working with visitors of all ages and backgrounds.

Advice to scientists regarding ISLO collaborations

Because science museums get so many requests from researchers to help them pursue the broader impacts portions of their research projects, I wrote a guide for science museum professionals several years ago, providing advice on ways to develop effective partnerships with university-based researchers and research centers (Alpert 2013). These days, I spend a considerable amount of time in universities, working with researchers on their professional and public communication skills, and I have learned that they often would like guidance about initiating effective collaborations with science museums and other ISLOs. The first lesson concerns last-minute calls.

Science museum managers often receive last-minute calls or emails from researchers who are about to submit a proposal to a funding agency such as the National Science Foundation. These callers suggest that as part of their federally-funded research they will provide to the science museum a great set of evening lectures, or perhaps an exhibit to be designed by their graduate students in connection with their proposed research. Typically, the university caller requests a pdf sent on museum letterhead, confirming commitment to the proposed collaboration. The request may be urgent, as the letter needs to be included in the proposal submission which may be due in only a few days; the details to be worked out later. Yet, by this stage in the proposal development process, the entire budget has almost certainly already been allocated. There has likely been little discussion on what form of outreach might be best suited to the topic or to the intended audiences, and no consultation with the proposed ISLO collaborator. As I advise my science museum colleagues, such a request needs to be politely but firmly turned down, with an invitation to make contact again several months ahead of the next proposal due date. Here are a few of the warning flags this approach raises in the mind of the ISLO professional:

- It is indicative of last-minute planning, and assumes either that public engagement projects are trivial to carry out, or that the museum already has plenty of funding, resources and staff on hand to do the work, which is almost never the case.
- In the absence of a budget and a well-thought-out evidence-based plan, savvy reviewers may doubt serious commitment. Even if the proposal is funded, neither partner will have much incentive to follow through on the vaguely-stated intent, especially in the midst of other more pressing priorities. This just-in-time approach does not bode well for future collaboration. It tends to produce token efforts, perhaps in time for critical grant reporting periods.
- Lectures and talks have their place in informal science learning settings. Even so, most university-style talks and Powerpoint presentations need considerable transformation before they are ready for prime-time in free-choice learning venues, where the audience will walk away if not engaged, or if the slides are crammed with graphs and technical information too small to see. Had the researchers proposed introductory discussions earlier with ISLO management and staff, there could have been brainstorming and collaboration toward crafting more welcoming, interactive, and effective audience engagement experiences.
- The conception, design, and production of most science museum exhibits is a complex, team-based craft of professionals guided by accepted standards in education, design, spatial integration, accessibility, and safety; with adherence to strict scheduling for prototyping, evaluation, and revision; and a commitment to maintenance. It is not a job for graduate students. However, with appropriate staff support, many museums can provide graduate students with training in science communication and public engagement, and work with them to develop smaller, simpler hands-on activities for visitors and other forms of face-to-face engagement.

The last-minute phone call signals a lost opportunity to benefit both the research enterprise and the broader community, the principal investigator and the students, and the cause of science literacy in general. But it does not have to be this way. Gradually, researchers and informal science educators are learning how to come together to brainstorm and plan their collaborations more effectively and successfully.

Collaboration through strategic planning

With inspiration, complementary expertise, and advance planning, many researchers and ISLO professionals have initiated very successful research center—science museum collaborations, some lasting for many years. I manage one that has been ongoing since 2001, funded by successive NSF research center grants and renewals (NSF 0117795, 0646094, 1231319). This collaboration has produced museum programs and presentations, videos, podcasts, and television news, science theater and special events reaching millions of people. It has also provided science communication training for hundreds of university students. But a successful collaboration need not be so grand in scale. What counts most is that the collaborators understand each other, discuss the options in advance, find the right fit for their respective interests, resources, and prospective audiences, agree on a plan of action, and set an appropriate budget. In smaller scale collaborations—for instance, those involving a single research lab and a local ISLO or a single department of a larger ISLO—these planning activities may be easily accomplished in the space of several meetings, culminating in a simple letter of agreement.

Larger-scale collaborations—such as those involving large research centers, multiple organizations, and ambitious projects to be implemented across several years—are more likely to succeed if certain planning steps are undertaken in advance. We recommend that each prospective collaboration partner conducts a preliminary strategic assessment that lays the groundwork for building successful collaborations. For the ISLO partner, this includes:

- identifying high priority topic areas for exhibit and program enrichment; especially those that would benefit from collaborations with university researchers and students; and
- providing infrastructure for vetting and managing collaborations. This may include designating a point person and setting up in-house procedures for internal planning, consultation, evaluating, and budgeting and accounting.

For the research partner, it includes:

- assessing the range of goals for pursuing the collaboration;
- considering desired outcomes;
- evaluating available resources or potential external funding;
- exploring potential partners and their interests and availability; and
- beginning discussions many months prior to the intended activity or proposal.

Translating research

Scientists get funding for very specific technical investigations that can sound quite inaccessible to general audiences. The research team may be proposing, for instance, to investigate how rainfall patterns influence fertility variations across sub-populations of a certain ground species. Science communication professionals and museum educators can help scientists tell their story within a broader context that provides additional motivation and relevance; perhaps in this case, the need to better understand the impact of climate change on the emergence of new animal-borne diseases. They might also encourage the researchers to share more personal insights, to highlight the adventures of field work, bring in samples, or develop an interactive activity that allows players to explore the effects of several variables on animal populations and disease. The goal is to balance the what with the why and the what for—to tell a good story and reveal the eye-opening big picture. The hidden benefit for scientists is that these strategies can also be quite useful in helping them communicate effectively with funders, journalists and, perhaps surprisingly, with scientists in other specialties, helping to set the stage for innovative cross-disciplinary research collaborations (Alpert 2013).

Forms of engagement

Most people think of exhibits when they think of science museums, and yet an exhibit may not be the best approach. Exhibits are expensive, and they take a lot of time to develop, prototype, test, and install. They are also difficult to update as the research advances.

Scientists who want to engage more actively with visitors would do well to conceive of it as an opportunity to learn as well as share expertise. By being willing to listen and ask questions, they can join with visitors in exploring broader aspects and societal implications of research, and these conversations can sometimes yield important new perspectives. If the research has controversial elements, tools are available to help researchers working with ISLOs develop public forums on science and technology topics (Bell et al. 2017).

Much interpretation of current science occurs in the form of museum exhibit hall presentations and demonstrations, through web and new media, and at special events where researchers and their students can interact and dialogue with visitors, preferably with prior coaching by ISLO staff. These types of activities are easier than exhibits to update and improve as the research progresses and yields new findings. In nature centers and zoos and aquaria, enrichment programs can also take the form of tours and gallery talks, aided by hands-on activities that bring visitors closer to the organisms and environments under study.

One of the best uses of grant resources is to provide partial support for one or more ISLO educators who can get to know the research team and their work, and collaborate with them to develop novel programs and activities. The ISLO educators can then deliver those programs and activities on an ongoing basis without taking too much time away from the scientists and their students. This strategy leverages the partnership to achieve even broader impact; many more people will have the opportunity to participate; there may be potential for further dissemination.

Budget

Try to avoid getting too far along discussing a vision for education and outreach without some grounding in the reality of its cost in relation to the resources available. If funding is limited, aim to do a fabulous job within the available resources; or, see if negotiation or additional fund-raising can produce the necessary resources. University faculty may be accustomed to a culture where time is more flexible and students provide off-the-clock labor. They may underestimate the true cost of the professional expertise involved in developing, testing, and carrying out truly effective informal science learning programs on a regular basis. The bottom line is to design a scope commensurate with the budget, and then execute it very well.

Research and evaluation

Research and evaluation are increasingly important aspects of informal science learning design, and the field is developing in a more scholarly way, with increased capacity to devise testable research questions, implement stricter protocols, and publish findings. Outreach collaborations do not typically involve formal research studies, but they do require a commitment to at least a literature review and front-end and formative evaluation strategies that can help guide the design, development and remedial modifications of exhibits and programs, workshops, and other kinds of learning activities. While page limits restrict the amount of detail allotted to the education, outreach and other broader-impacts components of research proposals, the plans will be taken more seriously if they (1) reference published material supportive of the approach, (2) include evaluation plans, and (3) mention the qualifications of the design and implementation team. Review panels and program officers are increasingly savvy about distinguishing well-planned, evidence-based strategies from those that merely sound good. They look for measures of impact and other forms of accountability that can be built into the program, as well as the intention to share what is learned through posting of evaluation studies to repositories such as www.informalscience.org. NSF has made available its own Framework for Evaluating Impacts of Informal Science Education Projects (Friedman 2008), and the NISE Network developed a Team-Based Inquiry Guide (Pattison et al. 2014), that helps program developers conduct their own in-house formative evaluations. Keep in mind that surveying, observing, testing, interviewing, and other evaluation protocols conducted with adults and particularly with children (minors 18 and under) may be subject to approval by an Institutional Review Board (IRB). Partners should be prepared to set up a working arrangement with the university's IRB or that of the ISLO.

A Worksheet for Scientists Seeking Collaborations with Informal Science Learning Organizations (Reproduced here with permission from the Museum of Science)

<u>What do we want to share with broader audiences?</u>

- Do we have specific messages to communicate? A new perspective to share?
- Why do we think it is important to share these ideas/experiences? What motivates us?
- How might the community benefit?
- Whom do we most want to reach, and where can we find them? What might we learn from them?
- Are they likely to already have an interest or connection to this topic?
- How will we attract and engage them? What unusual experiences might we be able to offer?
- What is our timeline, and what resources can we bring?

<u>What informal science learning organizations might we be able to partner with?</u>

- e.g., natural history, science, or children's museums; zoos, botanical gardens, aquaria; parks, historic sites, visitor centers; libraries, after-school, community organizations.
- What programs and activities do they have that we might fit in to?
- Who can we speak with there?

<u>Topics for discussion with a potential ISLO partner</u>

- Do they already partner with researchers? If so, what is the procedure?
- How interested are they in our topic area and our ideas for collaboration?
- What resources, materials, and expertise can we bring to the table? (What special experiences can we offer?)
- Could they help us develop the content and format in a way that will be successful with their visitors?
- What additional funding, resources, support will they need? Are they interested in joining a grant proposal with us, and do they have the wherewithal to do that? (e.g., grants management infrastructure, IRB, federal ID, etc.)

- Can some of our students be involved? What training will they need?
- What is a reasonable timeline for pursuing next steps?

Working together

- Designate coordinators from each organization.
- Meet to brainstorm ideas for developing engaging content and format.
- Check these against practical and operational constraints, time, and resources.
- If a funding proposal is required, come to agreement on scope and budget.
- Devise an initial development, evaluation, and implementation plan.
- Vet with internal and external stakeholders.
- Set timelines and checkpoints.
- Keep in touch. Regular communication builds trust and confidence.

Resources for scientists interested in partnering with ISLOs

- Find a science center, museum, zoo, or aquarium at the Association of Science-Technology Center's web resource: http://www.astc.org/about-astc/about-science-centers/find-a-science-center/
- Gain insight into informal science learning pedagogy, strategy, and evaluation at the Center for the Advancement of Informal Science's introductory page for scientists: http://informalscience.org/projects/scientists-and-public-engagement
- Consult the Framework for Evaluation Impacts of Informal Science Education Projects, an NSF-sponsored guide: http://www.informalscience.org/framework-evaluating-impacts-informal-science-education-projects
- Consult the website of the National Alliance for Broader Impacts (NABI), an NSF-funded network of individuals and organizations working to build institutional capacity, advance BI, and demonstrate societal benefits: https://broaderimpacts.net.
- Consult "Public Engagement with Science: a guide to creating conversations among publics and scientists for mutual learning and societal decision-making," at https://www.mos.org/sites/dev-elvis.mos.org/files/docs/offerings/PES_guide_10_20r_HR.pdf.
- Look into Portal to the Public, a network of ISLOs that provide training and resources for museum-university partnerships: https://popnet.pacificsciencecenter.org
- Download printed and electronic material included in the Sharing Science Workshop & Practicum Planning & Implementation Guide. The SSW&P is an effective one-day or two half-day workshop used by researcher-ISLO partners to introduce researchers and their students to inquiry-based learning techniques in informal science learning environments. http://www.nisenet.org/catalog/tools_guides/sharing_science_workshop_practicum

Share your science; give it a shot

Share your science. Learn to do it well. Do it with young people, old people, family members, community, and strangers. Share not just what you have learned, but also how you have learned it, and how it has influenced your way of thinking. Endeavor to show others why you find it fascinating, and what relevance it may have to our lives and to the world we live in. Invite others in to experience a bit of what you do. Encourage them to ask questions; reward them with responses formulated in simple terms, word pictures, and analogies. Be open to their thoughts and ideas and listen well. Such inspiration is priceless.

Acknowledgments

The author wishes to thank her Museum of Science colleagues Karine Thate, Megan Litwhiler, and Larry Bell; Martha Merson for the impetus to write this piece; and the reviewers for their sound advice.

Funding

This work was supported by the National Science Foundation [grant numbers 1231319, 1323030, 1555541].

References

Alpert CL. 2009. Broadening and deepening the impact: a theoretical framework for partnerships between science museums and STEM research centres. Social Epistemol 23:267–81.

Alpert CL. 2009. The research communication continuum: linking public engagement skills to the advancement of cross-disciplinary research. J Museum Educ 28:28.

Alpert CL. 2013. A guide to building partnerships between science museums and university-based research centers. Museum of Science, Boston: NISE Network.

Association of Science Centers (ASTC). 2017. Science center statistics from the 2016 ASTC Statistics Survey. (http://www.astc.org/wp-content/uploads/2017/09/ASTC_SCStats-2016.pdf) (Accessed January 27, 2018).

Falk JH. 2002. The contribution of free-choice learning to public understanding of science. Interciencia 27:62–65.

Friedman, A. (ed.). 2008. Framework for evaluating impacts of informal science education projects. (http://www.informalscience.org/framework-evaluating-impacts-informal-science-education-projects) (Accessed March 18, 2018).

Bell, L, Lowenthal C, Sittenfeld D, Todd D, Pfeifle S, Kunz Kollmann E. 2017. Public Engagement with Science. Museum of Science. (https://www.mos.org/sites/dev-elvis.mos.org/files/docs/offerings/PES_guide_10_20r_HR.pdf) (Accessed March 17, 2018).

MOS. 2017. Video interviews with Center for Integrated Quantum Materials graduate student volunteers at NanoDays 2017. Boston: Museum of Science digital archives.

National Science Foundation. 2018. Broader Impacts: Improving Society. (https://www.nsf.gov/od/oia/special/broaderimpacts/) (Accessed January 29, 2018)

Pattison S, Cohn S, Kollmann L. 2014. Team-based inquiry: a practical guide for using evaluation to improve informal education experiences. 2nd ed. (http://nisenet.org/catalog/team-based-inquiry-guide) (Accessed March 17, 2018).

Society for Integrative & Comparative Biology annual meeting program. 2018, January 3–7, San Francisco (http://www.sicb.org/meetings/2018/spdac.php) (Accessed March 18, 2018).

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 94–102
doi:10.1093/icb/icy010

Society for Integrative and Comparative Biology

SYMPOSIUM

Developing Interactive Exhibits with Scientists: Three Example Collaborations from the Life Sciences Collection at the Exploratorium

Denise King,[1] Joyce Ma, Angela Armendariz and Kristina Yu

Exploratorium, Pier 15, the Embarcadero, San Francisco, CA 94111, USA

From the symposium “Science in the Public Eye: Leveraging Partnerships” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1]E-mail: dking@exploratorium.edu

Synopsis Science museums have made a concerted effort to work with researchers to incorporate current scientific findings and practices into informal learning opportunities for museum visitors. Many of these efforts have focused on creating opportunities and support for researchers to interact face-to-face with the public through, for example, speaker series, community forums, and engineering competitions. However, there are other means by which practicing scientists can find a voice on the museum floor—through the design and development of exhibits. Here we describe how researchers and museum professionals have worked together to create innovative exhibit experiences for an interactive science museum. For each example: scientist as (1) data providers, (2) advisors, and (3) co-developers, we highlight essential components for a successful partnership and pitfalls to avoid when collaborating on museum exhibits. Not many museums prototype and build their own exhibits like the Exploratorium. In those cases, there may be similar opportunities in more mediated offerings such as public demonstrations or lectures or in other formats that allow for direct interactions between scientists and visitors. We believe there are many opportunities for researchers to share natural phenomena, to advise on exhibit development and interpretation, to provide much needed materials, and to otherwise incorporate authentic research into the learning experiences at museums, no matter what the format.

Introduction

Exhibits are the heart of a museum experience. In a science museum or center, they “present natural phenomena, technological innovations and scientific ideas in ways that prompt visitors, interacting with them, to ask themselves questions and reinforce their own learning” (Semper 1990, 50). They may also focus on aspects of scientific practice, allowing visitors to engage in inquiry with the authentic tools and techniques a practicing scientist would use. A museum exhibit experience has been described as episodic versus continuous, short—possibly a few minutes, and unmediated, without staff facilitating its use (National Research Council 2009). Because museums are free-choice learning environments, visitors may not encounter, let alone choose to attend to an exhibit, and exhibits are rarely used according to a planned sequence. Some exhibits may be organized into an exhibition with a strong, overarching message; others may be placed in a loose thematic configuration with neighboring exhibits. Thus, there are no guarantees that a visitor will come to an exhibit with the prerequisite knowledge learned from a prior exhibit to make sense of the current exhibit being used (National Research Council 2009). Finally, the museum is a social and physical place (Falk and Dierking 2012), where visitors come with family and friends to, increasingly, use hands-on interactive exhibits.

Although all museums curate their exhibit collections to fit with their mission, audience, and institutional priorities, not all museums are able or choose to develop their own exhibits. The three examples given in this paper are illustrations of what is possible when there is a development team at an institution, the Exploratorium, with a long history and commitment to prototyping. Museums without in-house exhibit development staff can use these examples to guide their relationships with local researchers, inform their work with outside consultants, and as inspiration to create their own exhibits and programs with researchers. Each example represents a different way in which research scientists worked with exhibit developers under multiple constraints to create an engaging exhibit for the museum floor: (1) researchers as data providers, (2) researchers as advisors, and (3) researchers as co-developers.

Background

Biology exhibits at the Exploratorium

The Exploratorium, founded in 1969 by Frank Oppenheimer, is an organization dedicated to creating inquiry-based experiences that foster curiosity about the natural world. The museum is located on the San Francisco waterfront where we create tools and experiences for our museum visitors, our online audience, local communities, teachers and other educators, and museum professionals. The public floor of our museum has over 600 exhibits in seven galleries loosely organized by subject matter. Many of these exhibits are interactive and almost all of them were built on-site in the Exploratorium's machine shop.

In addition to the machine shop, the Exploratorium has an on-site 3000 square-foot biology laboratory. The laboratory facilities include a sterile cell-culturing room, −80°C freezer, incubators, an autoclave, fume hood, laboratory benches, and safety equipment. It also houses dedicated plant-growing facilities, a zebrafish culturing facility, and a salt water table. The laboratory contains numerous dissecting and compound microscopes, including four research-grade automated microscopes in the Microscope Imaging Station (MIS) facility. Staffed by biologists, the laboratory cares for a living collection of over 40 types of samples, including fruit flies, human stem cells, mimosa plants, and an assortment of microbes. This facility is adjacent to the exhibit floor and is used to support new exhibit development and ongoing exhibit maintenance.

The following outlines the basic process used to develop biology exhibits at the Exploratorium (Fig. 1), with a focus on what may be helpful to potential scientific partners who wish to become involved.

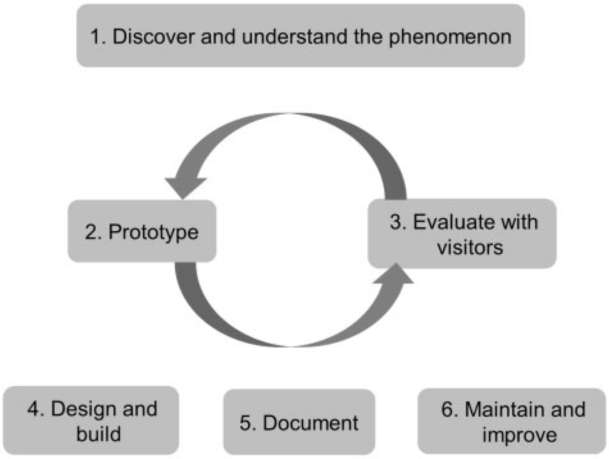


Fig. 1 Exhibit development process.

(1) Discover and understand the phenomenon. The first step to developing an exhibit is to identify a compelling phenomenon with which visitors can interact. Ideas can come from various places including research papers, classroom demonstrations, Internet searches, and art installations. Academic conferences offer a wide array of talks in a defined content area, as well as a way to meet researchers in person. Museum staff may not be members of multiple academic societies so access may be an issue. To bridge that gap, researchers can sponsor museum staff from their local institutions to attend a conference in a subject area they are currently exploring. Another very important way we identify candidate phenomenon is through visiting research laboratories. Lab visits allow us to see new phenomena and organisms, as well as the equipment necessary to maintain and interact with them. Inviting museum staff into research laboratories is a low stakes way scientists can support our work.

While searching for potential exhibit ideas, we constantly assess how well a potentially interesting phenomenon might translate to an exhibit. We ask hard questions prior to the start of prototyping and often depend on scientists to help us better understand the answers:

- Is an exhibit the correct outcome for the phenomenon, content, and concepts? Many concepts and content areas are very difficult to adapt to hands-on, phenomenological exhibits. If an idea is not well suited for a phenomenon-based exhibit, it is best to acknowledge this early and explore other options. Perhaps a live demonstration by a knowledgeable scientist would be more engaging to visitors or spark another exhibit idea?

- Is the interactivity of the proposed exhibit meaningful to visitors? Can visitors interact with the phenomenon, or is the interactivity solely designed to deliver more content or give the visitor something to do divorced from the actual phenomenon? Do visitors even understand that they are interacting with the phenomenon? This is a question that may best be answered by talking with visitors to ascertain their point of view.
- Can visitors experience the phenomenon? Is the phenomenon reproducible and at what time scale? Because many Exploratorium visitors spend less than 30 s at an individual exhibit, it is important for the phenomenon to be readily experienced upon approach.
- Is the exhibit experience worth the development effort and cost? For example, is the technology needed for the exhibit stable and affordable? Would this be the case in 5 years?
- If an exhibit successfully makes it to the museum floor, can it be maintained? Is there a local laboratory that is willing to support the exhibit with raw materials for the long term?

The length of time for this phase of a project can vary widely from 2 months for a single exhibit, to a year or more for groups of exhibits. Content that is more abstract, goals of funders and museum staff, and technical complexity can add time to this estimate. The best strategy is to discover more ideas than the number of eventual exhibits. Smaller museums may want to focus on developing fewer interactives which are supported with more traditional exhibitry.

(2) Prototype. Once these questions have been initially assessed, and we believe the idea is worth pursuing, we follow an iterative development process informed by visitor evaluation. We continue to ask these questions especially during the early stages of prototyping. At first, exhibit developers try out simple, mocked-up, mediated interactions to explore the phenomenon. If these initial interactions show potential, the exhibit developer does a deeper dive to develop her understanding of the phenomenon, often with scientists' help, and to determine ways to exhibit the phenomenon. Typically, there are several rounds of quick, low-cost prototyping with small groups of colleagues before it is tested with visitors for refinement.

(3) Evaluate with visitors. Once the exhibit developer has a prototype that she feels is ready for visitor testing, she starts a conversation with an evaluator to determine what type of visitor input would be useful and can be collected to inform the prototyping process. Evaluation is an integral part of exhibit development at the Exploratorium, used to understand visitors' interactions with a prototype, and identify potential issues and opportunities for improvement. Evaluation can help refine an early prototype as well as check a fully functioning version of a nearly complete exhibit before its final build. The Exploratorium's Visitor Research and Evaluation Department works closely with developers throughout the prototyping effort. Not all museums have in-house evaluators and may depend on outside consultants or other staff members. What is important is that usability issues and misinterpretations are identified and addressed and that often depends on talking and/or observing visitors systematically with the prototype.

Timing of prototyping and evaluation varies greatly depending on the complexity of the exhibit, both in terms of content and interactivity design. It is important to remember to keep the exhibit as simple as possible. Avoid incorporating multiple ideas and pathways in to a single design (Allen and Gutwill 2004). Expect to budget 3–4 months for a single exhibit, up to a year for more technically complex exhibits like Example 3. Smaller museums may want to work with local fabrication shops to assist in prototyping.

(4) Design and build. After multiple iterations, the exhibit developer converges on the final interaction design. The central focus of the design phase is to keep the interaction true to the prototypical form, while hardening the design so it can withstand the rigors of the museum floor. The exhibit components are often drawn and assembled in 3D modeling software so the vision of the exhibit developer can be shared with the project team. The design takes into account Americans with Disabilities Act guidelines, durability of materials, and standard components that have been used successfully in previous exhibits. Often, designs and components with proven durability become standards that are applied to future exhibits. If the exhibit is part of a larger collection, design elements and materials

may be shared among several exhibits. In our experience, we expect to budget up to 4 months per exhibit for design drawings, fabrication, and assembly. If working with outside fabrication shops, it may be best to bundle multiple exhibits into batches. Smaller museums can develop relationships with local workshops that may provide design help, or work with an exhibition design firm during the production phase of the project.

(5) Document. Once an exhibit is successfully installed and can be maintained on the museum floor, it is extensively documented and archived for future reference. Documentation can include pictures of early prototypes, fabrication drawings, background information on the scientific concepts in the exhibit, and a contact list of vendors and/or research scientists who have provided materials. Document early and often, and complete the documentation package within 2 months of the opening of the exhibition while the information is still fresh.

(6) Maintain and improve. At the Exploratorium, we like to think that no exhibit is ever truly "finished". Instead, we feel that most exhibits can be improved over time, as we learn more about visitors' interactions, with the evolution of technology, or with scientific advancement. However, limits on time and resources mean that revisions become few and far between as time passes and the focus shifts to exhibit upkeep. It is important to clearly communicate when the exhibit development project is complete and the commitment of the scientist is fulfilled. If the exhibit needs ongoing support such as live cultures, these should be clear and agreed to by the researchers and museum staff.

Example 1: Researchers as data providers

The following example from the development of the exhibit, *A* Cell in Motion, illustrates how researchers can share scientific data for exhibits.

Exhibit description

A Cell in Motion is a large, mechanical zoetrope that features 3D prints of a real cell crawling across a surface, imaged at the University of California, San Francisco (UCSF). A zoetrope is an 18th century device that creates an illusion of motion using a series of still images, or in this case 3D "sculptures." Recent advances in microscopy have made it possible to capture 3D images of live cells, which we were then able to 3D print using the original data. *A* Cell in Motion has 49 cell sculptures, each approximately 3.5 inches in length, representing about 2 min of the cell in motion. As a visitor turns a hand crank, strobes flash in time with the speed that the cells pass by, creating the illusion that a single cell is moving in three dimensions (Fig. 2A,B).

Components of a successful data share

Megan Riel-Mehan, a postdoctoral scholar in UCSF's Department of Bioengineering, serendipitously met an Exploratorium biologist at an academic conference and showed her a zoetrope movie she made using 3D data from the light sheet microscopy work of Dr. Lillian K. Fritz-Laylin from the Department of Cellular and Molecular Pharmacology at UCSF. The Exploratorium biologist shared the movie with an exhibit developer, who was inspired to make a physical version, envisioning the cells rendered as physical objects in a series. Dr. Riel-Mehan worked with the exhibit developer to optimize her data for the museum's 3D printer and to choose an appropriate sequence of images that would be printable at the Exploratorium. The key ingredients to this successful collaboration were Dr. Riel-Mehan's willingness to share her data visualization expertise and her data, which required a degree of trust since the scientific data had yet to be published when prototyping work began. The findings have since been published (Fritz-Laylin et al. 2017), and the contributions of the scientists are revealed to visitors in the exhibit label. All data sharing and communications were electronic, making this type of relationship amenable to geographically distant groups.

Example 2: Researchers as advisors

The example of the MIS project lets us look at the participation of the scientific community over the course of a multi-year project that focused initially on exhibit development but has evolved into an important programmatic cornerstone of the museum's biology collection.

Project description

The MIS project started with the goal of bringing the beauty and wonder of live microscopic samples to museum audiences. With developments in automated microscopy, it had become feasible to adapt research-grade, computer-controlled light microscopes for use by museum visitors. Previously, the use of such instruments had been primarily limited to academic laboratories at universities and other research institutions. The initial project proposal was developed by the Exploratorium in collaboration

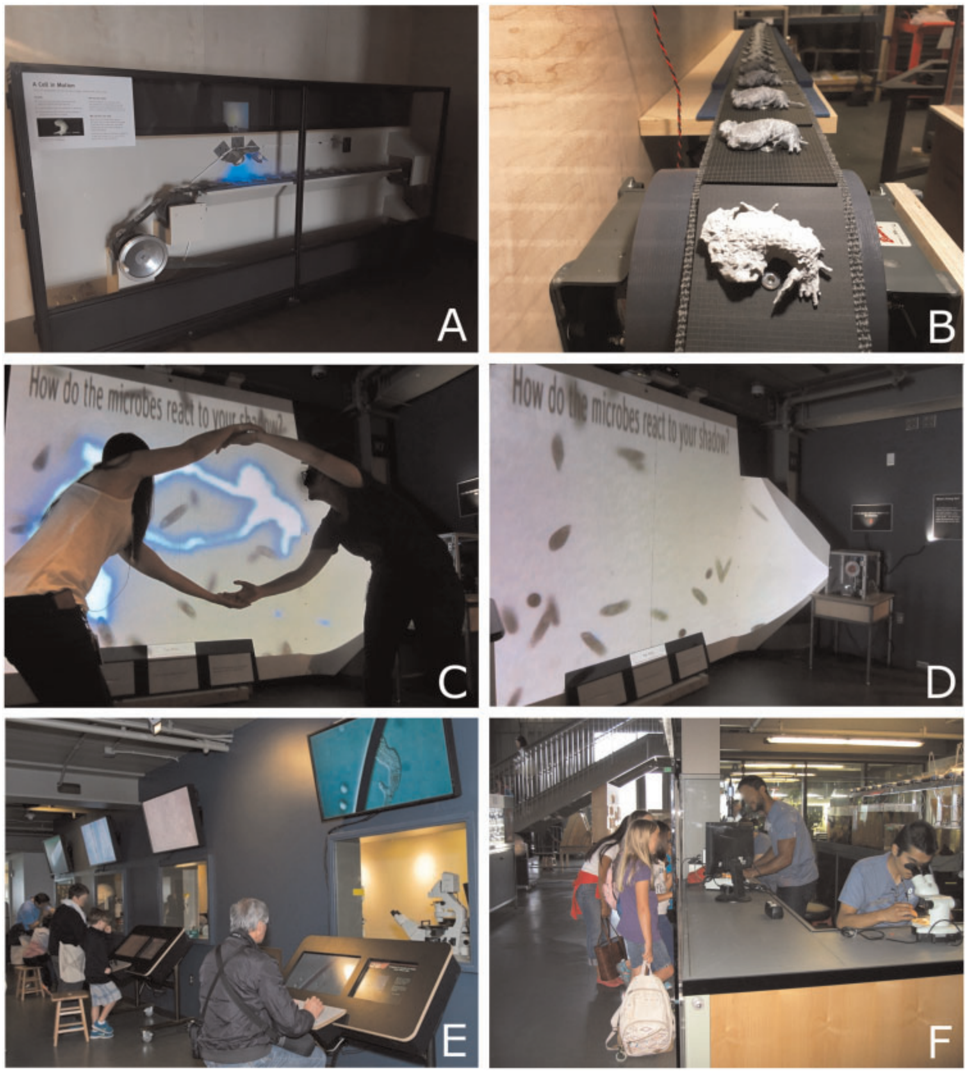


Fig. 2 Exhibit prototypes and facilities. (**A**) A cell in motion exhibit. (**B**) A cell in motion's 3D sculptures. (**C**) Two people using the VIM exhibit prototype. (**D**) The large projection and the microscope in the VIM setup. (**E**) Visitors using the interactive microscopes in MIS. (**F**) Scientists at work with visitors at the living systems laboratory facilities.

with a research scientist with a significant background and experience in microscopy, as well as a desire to reach the public with the imagery and sense of discovery that he found so compelling in his scientific work.

Housed in a room with large windows onto the exhibition floor, the MIS facility contains four automated, computer controlled light microscopes. There are currently three Zeiss MZFLIII inverted microscopes and one Zeiss AxioZoom, all with computer controlled stages, focus, objective change (or, in the case of the AxioZoom, a zoom), and light settings. On the outside of the facility, on the museum's public floor, are kiosks that enable museum visitors to "drive" the microscopes and look at a live, full color video direct from a microscope on a large screen. Visitors control the microscopes using a joystick to move the motorized stage, a knob to focus, and a touchscreen, where virtual buttons let visitors choose magnification, light conditions, and sample type. The microscope used by a visitor is in view through large windows, and the live image from the microscope also appears above the window on a large video monitor (Fig. 2E). All samples featured in the MIS exhibits are alive and may include developing zebrafish (*Danio rerio*) embryos, the protist amoeba, mouse embryonic stem cells, or cardiac myocytes derived from mouse embryonic stem cells. Adjacent to the live image, interpretive media guides visitors through sample exploration and provides context and information about the live sample in view.

Components of a successful advisory relationship

Advice from the research community was particularly valuable during the initial stage to help staff discover and understand the phenomenon and technology. This advice came in several forms:

Equipment expertise. During the initial phases of MIS development, choosing what hardware to invest in was critical. The advice and expertise of a number of project advisors were invaluable in pointing the museum team toward instruments that they as researchers and everyday users could recommend in terms of robustness and meeting the technical needs of the project. They also could speak from direct experience using these microscopes about ease of use and extensibility to studying a wide variety of live samples. The choice of key accessories for the microscopes, such as heaters, objectives, video cameras, and shutters, was also heavily influenced by the perspective of the project's research advisors.

Sample selection. Critical to the success of the "exhibit" aspect of the project and visitor engagement was sample choice and procurement. For this, the museum project team had the benefit of being in San Francisco. With a number of research universities as neighbors, proximity was key, enabling museum staff to visit a number of laboratories in search of suitable live samples for this suite of microscope exhibits. A number of researchers in the San Francisco Bay Area generously hosted visits so that the MIS project team could not only see the live samples in action in a scientific setting but could also have honest conversations with the scientists using the samples as to how feasible it might be to maintain the sample in the Exploratorium's laboratory. Once appropriate samples were identified, researchers were enormously generous in providing these live specimens to the museum to be used in the exhibit, or providing detailed information about where to obtain the samples and how to maintain them.

Scientific content and practice. Finally, with the instruments in place and live samples chosen, scientific advisors were asked about how they used the live samples in their basic research. These stories and in-depth scientific discussions became the backbone of the interpretive media that accompanies each live sample in the exhibit.

Example 3: Researchers as co-developers

The Visitors Interactions in Microbiology (VIM) project is a partnership between the Exploratorium and the Riedel-Kruse Bio-engineering Laboratory at Stanford University, which has pioneered hybrid digital-biological systems that allow users to manipulate microbial behavior. Both parties are co-leads and are co-developing the VIM exhibit prototypes. As such, of the three examples described in this paper, this represents the highest level of commitment and integration from participating scientists.

Project description

The VIM project aims to shed light on how biotechnology can be integrated into exhibits to allow real-time interactions with microscopic life at the human scale. Exploratorium staff and researchers from the Riedel-Kruse Laboratory met serendipitously during an academic conference. At the time, the Riedel-Kruse Laboratory had already built a prototype system, Trap it!, that allows museum visitors to draw images on a touchscreen, which are projected onto a microscope slide with live organisms, *Euglena gracilis*. These microbes are phototatic and, therefore, respond to the images projected from the human-scaled world. The microbes and the light drawing on the slide are, in turn, projected back to the touchscreen. An evaluation conducted on Trap it! indicated the possibilities of this system as a promising platform to introduce interactivity into biology exhibits (Lee et al. 2015). Since our chance meeting, the Exploratorium and the Riedel-Kruse Laboratory have worked together to adapt the original platform to create a physical, multi-user interactive experience for visitors (Fig. 2C,D).

Components of a successful co-development partnership

Agenda alignment. This co-development effort reflected a fortuitous alignment of the Exploratorium's and the Riedel-Kruse Laboratory's agendas. As a museum known for its hands-on exhibits, the Exploratorium is always looking for ways to create engaging, interactive experiences for its visitors. Interactivity in biology exhibits has been traditionally realized by providing observational instruments such as webcams or microscopes for visitor control, or hands-on models or computer simulations for manipulation. The biotechnology system prototyped by the Riedel-Kruse Laboratory offered a novel means of introducing a new form of interactivity into the repertoire of science exhibits in microbiology not just for the Exploratorium but for the larger museum field. At the same time, the Riedel-Kruse Laboratory had prototyped and evaluated its Trap it! platform and was beginning to look for other opportunities to adapt and use their system in informal learning environments. Working with the Exploratorium on a co-development project offered a means of using and refining their bioengineering work for learners in museums.

Complementary expertise. The Riedel-Kruse Laboratory brought deep expertise to the design and development of the biotechnology system used for VIM, while the Exploratorium staff has decades of experience building, prototyping, evaluating, and maintaining interactive science exhibits. Nonetheless, everyone on the VIM project learned enough about the prototype, the enabling platform, and the visitor experience to work together to strategize next steps, make informed decisions, tweak the experience when necessary, and keep the prototype running during critical stages of testing.

Each party's expertise was brought to the fore at different stages of the exhibit development process:

(1) Discover and understand the phenomenon. The Riedel-Kruse Laboratory has extensive experience working with *Euglena* and knew the minute details of their phototactic response to different light wavelengths and intensity as well as their upkeep. The Exploratorium staff had less extensive knowledge but learned through working with the research scientists to recognize the different microbial reactions to different lighting conditions, generate early ideas for visitor interactions, and ways to maintain samples at the Exploratorium that would reliably respond to stimulus.

(2) Prototype. The Riedel-Kruse Laboratory designed and developed the biotechnology platform and therefore knew not only how the platform worked and could be adapted but the history of what had been tried and why a particular solution may or may not work. Throughout the co-development effort, they held the deep expertise on the biotechnology platform, and as such, drove the redesign of the system. This included making design decisions, securing parts, and putting together multiple versions of the prototype.

    Meanwhile, multimedia exhibit developers at the Exploratorium brought their expertise in using existing and emerging technologies in exhibit development and public installations to the prototyping effort, taking the lead in the design and development of the Kinect-based user interface and projection displays. The tight integration between the platform and the user interface required very close collaboration between the Riedel-Kruse Laboratory and the Exploratorium, with clear understanding of the two subsystems' interface.

(3) Evaluation with visitors. For the VIM project, evaluation ranged from informal observations done by Riedel-Kruse researchers and Exploratorium developers, to more formal studies with visitors conducted by Exploratorium evaluators. Through a cycle of prototyping and evaluation, the VIM team built a shared understanding of how the VIM exhibit would work with visitors in the museum setting, grounded in the Exploratorium's past experience with exhibits, refined by technical testing of the VIM prototypes on the museum floor, and informed by visitor reaction and feedback. For example, the iterative process led us to select an eyepiece that could accommodate children who tend to have difficulties positioning themselves to see through the oculus. The light stimulus was carefully calibrated to effect a response from the Euglena that was meaningful to visitors who do not have the experience to readily recognize evasive behavior. And, the system was redesigned to address situations where continuous use by visitors drove away all the Euglena from the active field of view.

Onsite work. One critical aspect of co-development was the need to do some of the prototyping onsite. It was not the case that the researchers could build the prototype in their laboratory and install it on the museum floor. This was especially true for a system that needed to be fine-tuned to the light levels, the environmental conditions, and visitors' creative and frequent interactions. We also learned that given the complexity of the system, even trained staff at the Exploratorium could not easily step in and debug the system should something fail. Having a science partner that was in close proximity made rapid prototyping and debugging possible. Even so, we found it helpful to develop a system that allowed the researchers to remotely control the prototype and processes by which data from the physical prototype could be automatically recorded and transferred at the end of the day to the research laboratory for closer analysis to assess calibration levels.

Ongoing work. The VIM project is a work in progress with evaluation, design and build, documentation, maintenance, and improvement, still ongoing. The goal is to work out the prototype's technical issues with the Riedel-Kruse researchers, determine the best-case use scenarios for visitors, then proceed to the design, and build phase with the Exploratorium taking the lead.

Conclusion

This paper describes several ways in which research scientists have participated in the exhibit development process at the Exploratorium including: hosting laboratory site visits, providing materials (e.g., reagents, data, software, specimens), advising on scientific content and technology, co-developing exhibits and technology platforms, and co-writing exhibit development proposals. Although different types of participation require different levels of time and resource commitment, we have found it useful for both parties to consider the following before agreeing to work together:

- Do the parties' agendas align? At the very least, do the scientists believe they are contributing to something worthwhile at the museum and that their participation is meaningful? Sometimes exhibit prototypes fail and need to be abandoned. Is this an acceptable outcome for the researchers? Alternatively, does the work proposed fit with the timeline and institutional priorities at the museum?
- Is there a shared understanding of roles and responsibilities? And, can all parties commit the time and resources required? People outside of the museum field are often shocked at the time and money involved in taking an idea to a fully functioning museum exhibit. Are both parties clear on the process, what is expected of them, and realistic about what they can bring to the effort?
- Are both parties dedicated to cultivating a long-term relationship? In any collaboration especially between very different professional cultures, both groups need time to establish a common language and learn to communicate with each other. We have often found that thinking of a collaboration, no matter how short, as part of establishing and maintaining a long-term relationship helps both parties invest in not just the project but in each other and makes working together easy and fruitful, sometimes leading to additional opportunities.

Not many museums prototype and build their own exhibits like the Exploratorium. In those cases, there may be similar opportunities in more mediated offerings such as public demonstrations or lectures or in other formats that allow for direct interactions between scientists and visitors. For example, during Scientists at Work days at the Exploratorium, biologists are invited to set up, as they usually would in their own laboratories, in an open-air laboratory space adjacent to the Living Systems laboratory facilities inside the museum, and carry out their experiments for visitors to witness (Fig. 2F). They do not give a scripted demonstration but instead conduct authentic research in public view. Low, glass panels between the laboratory bench and the museum floor allow for the scientists to stop and have conversations about their work with interested visitors. Signage, produced in collaboration with museum staff, is used to attract visitors, but text is kept to a minimum to simply highlight the big picture goals of the research, and to depict the logos of the research organizations. We hope that Scientist at Work days not only provide the public insight into the authentic practice of science but also offer scientists and visitors a means to interact in personalized and meaningful ways. These interactions often allow for the researchers to share their personal stories about their science careers, and help to humanize the practice of science for our audiences. For more information on forming partnerships between researchers and informal science learning centers, we recommend Carol Lynn Alpert's A Guide to Building Partnerships between Science Museums and University-Based Research Centers (Alpert 2013).

We believe there are many opportunities for researchers to share natural phenomena, to advise on exhibit development and interpretation, to provide much needed materials, and to otherwise incorporate authentic research into the learning experiences at museums, no matter what the format.

Acknowledgments

We would like to thank the generous communities of researchers and scientists who have contributed to the exhibits and projects described here. For the MIS project, this includes: Kevin Elicieri, Christian Sardet, Stephen Smith, Fred Wilt, Fabrice Roegiers, Dyche Mullins, Bruce Conklin, Didier Stanier, Orion Weiner, William Sullivan, Nico Stuurman, Nenad Amodaj, and Thierry Brassac, among many others. *A* Cell in Motion was made possible with help from Lillian Fritz-Laylin and Megan Riel-Mehan. The VIM project depends on the dedication and talents of Amy Lam, Ingmar Riedel-Kruse, and Seung Ah Lee. And, Jaime Jahncke and Meredith Elliot from Point Blue coordinated the many scientists who kindly share their experiences as part of Scientists at Work.

Funding

This work was supported by the National Science Foundation [DBI 1548297; DRL 1612831; DRL 1514612]; the National Institutes of Health [NIH R25 RR15627]; the Gordon and Betty Moore

Foundation; the David and Lucile Packard Foundation; and Genentech.

References

Allen S, Gutwill J. 2004. Designing with multiple interactives: five common pitfalls. Curator 47:199–212.

Alpert C. 2013. A guide to building partnerships between science museums and university-based research centers. Nanoscale Informal Science Education Network.

Falk JH, Dierking LD. 2012. The museum experience revisited. Walnut Creek, CA: Left Coast Press, Inc.

Fritz-Laylin LK, Riel-Mehan M, Chen BC, Lord SJ, Goddard TD, Ferrin TE, Nicholson-Dykstra SM, Higgs H, Johnson GT, Betzig E, et al. 2017. Actin-based protrusions of migrating neutrophils are intrinsically lamellar and facilitate direction changes. elife 6:1–25.

Lee SA, Bumbacher E, Chung AM, Cira N, Walker B, Young J, Starr B, Blikstein P, Riedel-Kruse IH. 2015. Trap it!: a playful human-biology interaction for a museum installation. Proceedings of the 33rd Annual ACM Conference on Human Factors in Computing Systems, pp. 2593–2602. ACM.

National Research Council. 2009. Learning science in informal environments: people, places, and pursuits. Committee on Learning Science in Informal Environments, Board on Science Education, Center for Education, Division of Behavioral and Social Sciences and Education, Washington, DC: The National Academies Press.

Semper RJ. 1990. Science museums as environments for learning. Phys Today 43:50–6.

Integrative and Comparative Biology
Integrative and Comparative Biology, volume 58, number 1, pp. 103–112
doi:10.1093/icb/icy016
Society for Integrative and Comparative Biology

SYMPOSIUM

Species Loss: Exploring Opportunities with Art–Science

Jennifer Harrower,[1,*] Jennifer Parker[†] and Martha Merson[‡]

*Department of Environmental Studies, University of California—Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA; †Department of Art, University of California—Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA; ‡TERC, 2067 Massachusetts Avenue, Cambridge, MA 02140, USA

From the symposium “Science in the Public Eye: Leveraging Partnerships” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1] E-mail: jharrower@ucsc.edu

Synopsis Human-induced global change has triggered the sixth major extinction event on earth with profound consequences for humans and other species. A scientifically literate public is necessary to find and implement approaches to prevent or slow species loss. Creating science-inspired art can increase public understanding of the current anthropogenic biodiversity crisis and help people connect emotionally to difficult concepts. In spite of the pressure to avoid advocacy and emotion, there is a rich history of scientists who make art, as well as art–science collaborations resulting in provocative work that engages public interest; however, such interdisciplinary partnerships can often be challenging to initiate and navigate. Here we explore the goals, impacts, cascading impacts, and lessons learned from art–science collaborations, as well as ideas for collaborative projects. Using three case studies based on Harrower’s scientific research into species interactions, we illustrate the importance of artists as a primary audience and the potential for a combination of art and science presentations to influence public understanding and concern related to species loss.

Introduction

Societal activities that dramatically alter the planet and lead to species loss will continue, without key changes to policy and human behavior (Newbold et al. 2015). The frightening rate of species loss is galvanizing some into action, but possibly not enough to make a difference (McKibben 2011). Environmental organizations raise funds, file legal challenges, and apply political pressure, while most scientists will diligently continue their work, documenting species responses, quantifying species decline, monitoring habitat change, and destruction. This work is undeniably important. Nevertheless, without changes to policy and human behavior, societal activities that dramatically alter the planet and lead to species loss will continue (Daily and Ehrlich 1999; Novacek 2008; Newbold et al. 2015). Interdisciplinary collaborations are recognized as an important approach to address complex environmental problems (Frodeman et al. 2017) and are compatible with the emphasis on broader impacts that funders want to see scientists achieve. For those scientists who have no interest in stepping into politics, policy, or citizen science, but who can imagine motivating others to do so, we describe art (art making, art exhibits, art-led outreach) as one vehicle for spurring societal change.

Scientists do communicate their findings, typically publishing and presenting once data are in and analyzed. However, Harrower has initiated several outreach projects before completing her fieldwork, desiring to engage people now in attending to ecosystem health and communicating the urgency of species decline. This unorthodox approach is viable for projects that rely on discussions of species interaction and species loss, rather then specific findings about research sites. Further, by gathering feedback from audiences and art-collaborators during the research process, she ensures the development of engaging products and experiences for a variety of audiences. It is worth noting that such projects can qualify for institutional support—residencies that lend credibility to the effort and facilitate research permit approval, funding to support artists’

Advance Access publication May 19, 2018

involvement, and, in Harrower's case, approval from her dissertation committee to pursue outreach alongside her scientific research.

Art can connect people to complex concepts at an emotional level and could be used to increase public understanding of the current anthropogenic biodiversity crisis (Harrison and Harrison 1993; Jacobson et al. 2007; Ballengée 2015; A'Bear et al. 2017; Curtis 2017). Art has the potential to influence values, beliefs, knowledge, and the development of societies (Belfiore and Bennett 2006) which are the same factors driving the environmental behavior of citizens (Jackson 2005). Art can create a space for dialogue around important issues, and harness the power of narrative and imagery to deliver educational messages that could inspire aesthetic appreciation and emotional response (Carlson 2000; Curtis et al. 2014). Interdisciplinary teams can tap into a variety of professional and personal networks, enabling access to more diverse audiences for whom the science work alone may not have emotional resonance (Curtis et al. 2014; Ballengée 2015). The art making process can also enable a deep emotional connection to the subject being studied, and can build empathy and understanding around science concepts, organisms, and ecological systems (Kay 2000; Curtis et al. 2014; Ballengée 2015). As influential as art can be, as enormous as the potential rewards are, scientists have cause to be wary.

Analyses of art–science work have found both the quality of the art and the representation of the science lacking, which can do damage to the reputation of art–science projects (Ballengée 2015), and to the reputations of those who are involved in them. The default model for art–science collaborations can leave either or both parties unsatisfied, with a lingering sense of missed opportunities. In a common scenario, artists are hired help, carrying out an illustration of someone else's vision (Glinkowski and Bamford 2009). Or in some cases, scientists find their work becomes watered-down or misrepresented in the final art form (Glinkowski and Bamford 2009; Curtis et al. 2014; Miller 2014). However, if collaborators can achieve interdependence, the work can flourish. Interdependence refers to a clear understanding of roles, and dependence on the other to fulfill those roles (Bronstein 2003). Acknowledging that in a collaboration, individuals will not necessarily have full autonomy over timeline, team members, tasks, and technique, we wondered to what extent these could or should be negotiated. Pink's description of these four ts (team, time, task, and technique) is the basis for understanding intrinsic motivation. With autonomy over these areas, many people will feel motivated to produce at a high level (Pink 2011). By giving collaborators autonomy over two or more ts could lead to increased motivation and better collaborative outcomes. Avoiding the pitfalls requires high levels of engagement from all partners, a commitment to identifying a shared goal and buy-in for a shared aesthetic and oversight by scientist experts.

In this article, we describe scientist and artistic partnerships through three case studies of Harrower's eco-art projects, with additional supporting literature. There is a rich history of ecological and social practice artists who make provocative work that challenges people to care for their environment (Gablik 1991; Harrison and Harrison 1993; Miller 2014; Curtis 2017). Ecological artists utilize symbols and narratives of the nature/culture interface to actively engage the public to reckon with current social and environmental issues. These artists work across multiple disciplines to collaborate and utilize different cultures of practice through research, maker ecologies, scholarly publications, and art exhibitions.

Since navigating collaborations for purposes of communication science to public audiences is a high-risk, high-reward endeavor, we look at three case studies to answer the following questions: What features of the collaboration insure both scientific integrity and satisfying, creative roles for participating artists? What cascading impacts resulted from campus-initiated art–science collaborations? What are the benefits to soliciting feedback from the public during the creative process?

Case studies

Harrower's research explores the species interactions of Joshua trees and their mutualists—fungi and moths—and how the outcomes of those relationships could shift with the changing climate, resulting in population declines of the charismatic Joshua tree. Working as an ecologist, and multi-media eco-artist, she is interested in exploring through art how to visually communicate the complexity and ecological importance of symbiotic interactions (www.JuniperHarrower.com). Harrower is not alone in deriving inspiration for her scientific and artistic projects from national parks. The US National Parks have a long history of attracting and inspiring artists, from the early painters in the 19th century who were instrumental to establishing National Parks and attracting visitors, to the more recent widespread establishment of numerous artists residencies (Winfree and Dunaway 2011).

Harrower's work examines if we can influence education, empathy, and human desire to care for natural systems and organisms through art. She uses current science methods and multi-media art practices to investigate the outcomes of human influence on ecological systems. By approaching her study system through art and science, she hopes to better understand the form and function of the organisms as well as to share with others the hidden beauty of these threatened species interactions. Through this work she aims to encourage dialogue around social and environmental issues, to contribute to science theory, and to make thoughtful recommendations for policy and management.

The following three case studies from Harrower's interdisciplinary research were chosen to highlight examples of art–science collaborative work: a collaboration between artists and scientists in developing an educational art–science project for the classroom; an educational multimedia animation collaboration between artists and a scientist; and a large participatory art collaboration between artists, a scientist, park rangers, and the public to populate an online dating site for Joshua trees. An important measure of the impact of art–science projects can be gathered from participant and audience experiences (Neff et al. 2010; Curtis 2017). We include data and feedback that were gathered from surveys with 121 people across these studies. Surveys were a mixture of close-ended and open-ended questionnaires administered by Harrower on paper directly following an event or class, or conducted online with SurveyMonkey within days of the event. Open-ended responses were categorized and coded for further analysis (Mason 2017).

Project: seeking symbiosis

Seeking symbiosis grew out of Harrower's interest in increasing visibility for her ecology research among undergraduates enrolled in University of California, Santa Cruz (UCSC). Harrower and art faculty member Geoffrey Thomas co-led an undergraduate digital arts and storytelling class, teaching students about the symbiotic interactions of Joshua trees. As part of the class, Harrower introduced students to her laboratory, protocols and methods, as well as to the experimental seedlings. Students spent time in the greenhouses observing and sketching. Students created triptychs of the Joshua trees and processes of the symbiosis, with the goal to emotionally connect with viewers about tree loss (Fig. 1). Harrower and Thomas planned a showing of students' work on campus in both science and art spaces at the (UCSC), at a sustainability festival at UCSC, and shared via local press.

Cascading impacts

The outcomes from this collaboration include student and instructor art, an art/science education model, and exploratory art themes of Joshua trees and climate change that influenced collaborators work trajectories. The student artwork was exhibited in both the science and art departments, and Harrower and Thomas shared their collaborative model for art–science education at the California College of the Arts, art and science conference. This led to lively conversation with over 80 educators, scientists, and artists, who were interested in incorporating this education model into their classrooms and practice. These works were also presented and discussed at the 2015 UCSC social fiction conference. Images from this collaboration are now being used by park interpretive rangers in JTNP for educational outreach to teach Harrower's research to the public. With over 3 million visitors per year at JTNP there is great potential for wide exposure to these materials. Thomas created a series of images to consider social–political impacts of Joshua trees and climate change. One striking image of tarantula inspired mobile robots that housed Joshua tree saplings that was further developed and later influenced the creation of a stop motion animation about Harrower's research in JTNP.

Impact

Through anonymous feedback (end of class evaluations and an online survey), a majority of students reported that they gained a deeper understanding of the human forces driving biodiversity loss and climate change ($n = 19$). All students found the inclusion of science to be important and useful in their arts training (on a rating scale with strongly agree to strongly disagree). A number of students expressed the desire for a deeper understanding of the science and science methodology than we had the ability to cover in the class time, and felt that it would have greatly improved their ability to make meaningful art. In spite of the several hours invested in science content, some students remarked that their ability to engage with the concepts was limited to just illustrating the science.

Lessons learned

Harrower and Thomas articulated an assignment for their students' art projects that would grow out of learning about Joshua trees and stretch beyond

Fig. 1 Four examples of the projects from Harrower's art–science collaborations. (**A**) Seeking Symbiosis: Thomas' ghostly Joshua tree depictions with missing limbs reference the trees that we are loosing to climate change using the format of a triptych to commemorate death and dying. (**B**) Joshua Tree Love Story: Image still from the stop-motion animation that follows Harrower and her son on a research expedition through JTNP, to understand why the trees are dying. (**C**) Hey JTree: Online dating site to meet Joshua trees aimed at connecting the public to ecology research and to inspire love and stewardship for the trees. (**D**) Joshua Tree Love Story: Two backdrops used in the animation painted by Harrower's unique art process that combines elements of her research organisms into the painting process (such as Joshua tree seed oil and fibers) to achieve a deeper connection to the study system.

illustrating the symbiotic relationships. Once students were steeped in the factors affecting Joshua tree loss, and particularly the impact of climate change on key symbionts, students were encouraged to explore larger themes. They explored theories of the nature/culture divide, linking them to the current disconnect between human activities and their impact on species and ecosystems through visual imagery as desert caretakers. They invoked technological imagery and the cultural perception that in the end science will save us, and we don't need to dramatically change our behaviors (Jackson 2005). Students' responses confirmed the value of the approach Harrower and Thomas took to jointly develop a course rather than limit Harrower's science to a one-time guest lecture. As identified in other art–science projects, a reoccurring theme is some need for artist autonomy over the final project, to build intrinsic motivation and emotional investment (Glinkowski and Bamford 2009). To address students' feedback, future courses will allocate more time to exploring science content and give students a chance to propose projects inspired by the science that they work on throughout the length of the course.

Project: Joshua tree love story

The goal of Joshua tree love story is to increase the knowledge of an all-ages audience that might not attend a science talk or ranger program, with an animated, short film (available online and in classrooms) on species interactions. Additionally, to move artist collaborators and viewers to consider issues of species loss and motivate sustainable behaviors. We asked: can involvement in a science-rich animation project deeply connect artists to complex science concepts and motivate sustainable behavior? Can an animation convey key knowledge about science issues and motivate an emotional response among viewers? How does a pilot audience react to a science talk vs. animation?

Film is one of the US's widest-reaching art forms. Exported globally, a giant in the economy, the film industry touches millions of people. In spite of the popularity of homegrown videos such as YouTube, scientists rarely create educational videos about their work. But with reasonable fears of Joshua tree extinction, Harrower was interested in using film as a means to achieve her goals of increasing awareness and motivating action to mitigate climate change. Harrower found she could both control the storyline and trust collaborators to carry through on a vision that didn't dilute the science content or overly-dramatize the science process.

In order to make viewers feel the impact of species loss, the film rapidly portrays Joshua tree loss using illustrated and animated imagery. The animation written and directed by Harrower explores the unseen world of species interactions and challenges stereotypes of what science and scientists look like (Fig. 1) through the character of a scientist and mother (Harrower) doing field research with her baby. To motivate sustainable behaviors, the story connects with the viewers on a human level, through the relationship of a mother and her child. The narrative follows Harrower and baby on a research expedition across her field sites in JTNP to investigate if the rapidly changing climate is having an impact on tree survival, and to explore the intricacies of the species interactions that the tree depends on. Tiny yucca moths (as large stop motion puppets) appear in magnified detail. Viewers witness the moths stuffing pollen gathered in one blossom into the blossoms of another tree. The microscopic web of fungal interactions in the Joshua tree root system comes alive with clay and glass beads, symbolizing nutrient transfer from the soil via the fungi to the plant, in exchange for plant sugars. Viewers see trees across the set wither and die. The impact of the loss is heightened by the parallel aging of the baby into an old man, to emphasize that species loss can occur within a human lifetime. One way the film stays close to the science is by incorporating Harrower's highly detailed paintings that mimic the microscopic complexities of the underground Joshua tree and fungal symbiosis. The paintings are created from fibers and oils from the Joshua trees, matching the data collected in JTNP along a climate gradient from low to high elevations. The paintings give viewers a way to see how relationships change with local climate and soil conditions (Fig. 1).

Significant time was put into sharing knowledge about the science and the art needed to create the work. Harrower led visits to the field, laboratory, and greenhouses, and shared knowledge verbally and informally, through written reports, and used conceptual models and drawings. This fueled the interdependence of team members. The long hours shared together generated friendship and respect. Harrower clarified expectations at the beginning, such as a general timeline, baseline pay, and individuals' roles. These necessarily evolved throughout the project, with some team members having to take on more work, but additional funds were secured so participants felt their time was respected. Work was most productive when the team met together, otherwise momentum was maintained by weekly email reports and occasional small group meetings.

Impact

Informal educators struggle to capture the impact of widely shown or televised media projects. Can a film affect viewers' understanding of complex ecology and motivate behavioral shifts? To begin to answer these questions, Harrower convened a focus group that heard a science talk about the research and watched an early release version of the animation.

Joshua tree love story was screened at SymbioStudio (Oakland, CA, USA), following a science talk about the same research to 45 people. During the event, Harrower collected feedback via an anonymous survey (10 questions, close-ended, and 1 open ended question). Ninety-five percent ($n = 45$) of respondents felt the animation was more successful than the science talk at conveying the ecological information. Sixty-eight percent of those surveyed reported that they were moved to change their own potentially environmentally destructive behaviors after seeing the animation. Hundred percent of respondents agreed that the science talk was more powerful with the accompanying animation, and that likewise, the animation was more powerful having followed the science talk. Twenty-nine respondents provided thoughtful and lengthy descriptions for ways to improve the flow of the animation, identified areas needing improvement, or pointed out unclear artistic metaphors that were at odds with the scientific principles. Participants expressed that the emotional messages conveyed through the art connected with them on a deeper level than the science alone, and that this resulted in a stronger sense of urgency and need to do something about human behaviors that contribute to species decline.

Cascading impacts

Scenes from Joshua tree love story are part of a visual library that was created by Harrower during her iSWOOP residency at JTNP, to provide park interpretive rangers with materials for use in public education and outreach. The animated film will be shown at the JTNP Visitor Center, which during peak visitation serves as many as 4500 people in 1 day (personal communication from park staff). Park rangers may use film artifacts: dioramas, puppets, dolls, and props in a Visitor Center exhibit or as props during programs. We are also currently developing Common Core ecology and art lesson plans for educators to use in conjunction with this animation.

Through an anonymous survey and informal interview, collaborators ($n = 10$) reported that participation in an art–science project had inspired new methods and insights in their own work, and had also provided them with a deeper understanding and appreciation for current issues surrounding biodiversity loss and climate change, as well as appreciation for the science process. All participants felt their career was positively enhanced through this work. Following this experience, seven of the artists went on to participate in other art–science collaborations.

Lessons learned

All collaborators agreed on the goals to emotionally connect the viewers to issues of species loss and motivate sustainable behaviors. The techniques for art making, animation, and style (dolls and set design) evolved with artists' input. Artists also shaped the timeline and recruited colleagues to join the project as needed. So the shared vision or task, timeline, techniques, and even team were a joint effort. Because Harrower wrote the screenplay and gave orientations on the science, she controlled the accuracy and integrity, while granting artists freedom to create something beyond her original vision.

Significant effort was put into teaching all team members the science processes that informed the art, allowing for greater discourse between collaborators on design elements and the ability to brainstorm techniques for animating some of the complex biology. Unanimously, participants agreed that the voice of the artist was respected through the collaborative process.

Institutional support was critical to the creative and financial aspects of the project. Harrower credits Parker who advocated for outreach as and arts research as an academically important complement to her ecology research. Parker provided critical feedback on different elements of the work and access to resources, funding, connection to collaborators and space. The design team from iSWOOP, where Harrower works as artists-in-resident as well as a featured scientist, also contributed feedback and financial support to the project. These many different support structures gave the project academic validity and resources.

Gathering audience feedback was pivotal in guiding our final editing process. Further, the feedback that the animation was enjoyable and enhanced when paired with a scientist's talk has shaped how we think about disseminating the film. We intend to create a recorded talk as an alternative to an in-person presentation.

Project: Hey JTree

Hey JTree is an ongoing participatory art research project using social media, and an on-line dating site for meeting Joshua trees (Fig. 1). The goal of Hey JTree is to actively enhance interaction between research, visitors to the park, and on-line audiences with collected data from individual trees using text, photographs, art, and short video clips of charismatic Joshua trees set to music. Social media takes the notion of adopting a tree or an animal to a whole new level. Rather than being assigned a tree or adopting a generic wolf, the concept of online-dating enables people to emotionally adopt a specific Joshua tree that lives in JTNP. The need to counteract irresponsible social media posting by visitors is vast and urgent. Visitors show violations of rules that are intended to promote conservation. Images such as drone usage, feeding/touching animals, rock or tree graffiti, and climbing Joshua trees have been described by park staff as one of the most difficult challenges they currently face as managers (personal communication).

This project was envisioned by Harrower, who advertised through social media artistic networks and selected 53 visual artists, musicians, and writers to collaborate. This is the first cohort of citizen artists, by which we mean those who express ideas through the arts to achieve societal change, but who are not by training or vocation professional artists. But in time elementary students and others will take a turn at contributing art to this project. As citizen artists, they will create poems, prints, and record songs specific to their chosen Joshua tree.

A project website (www.heyjtree.com) details the ecological tree information for each individual, shows on a map where each tree lives, art, and music created for each tree, and includes a dating style profile (similar to on-line dating sites) written by professional writers. Collected data include details on tree height and branch number, to link with the moth and fungal data collected by Harrower from her research sites in JTNP. Each tree's location is given in latitude and longitude, but also recorded as a "scavenger hunt" and given in miles to drive and number of steps from identifiable locations in the park. The public can also participate as "citizen artists" by submitting "love letters," poetry, music, or art to their tree, which will be uploaded to the project site generating a collective shared love and experience for individual trees.

Lessons learned

The collaborative process was predominantly researcher driven, but benefited from space made to discuss possibilities and to let the project evolve with collaborators. Harrower hosted an art–science event at SymbioStudio where she gave a research talk and invited all collaborators to meet each other, learn about the research, and to brainstorm ideas. At this event, new ideas were born, that included: working with students through a creative writing class at UCSC to build additional tree correspondences, choosing a tree to promote that is on an educational tour led by JTNP interpretive rangers so they can describe and promote the project to the public, and other ideas for future art show displays that highlight the art, music, education, and tree ecology.

Citizen artists met with Harrower in her field sites and were trained to collect data for the trees, including height, branch numbers, location, photos, and video. This information was passed to the writers who then developed a character description for each tree. Writers were given almost complete freedom to create this work, as long as the writing was family friendly. Musicians each chose a tree, and were given complete freedom to create music for a 1-min tree video for their tree.

The visual artists' work, however, was more constrained. During the group meeting session at SymbioStudio, collaborators decided that a united image would be the most powerful for a future exhibition setting, and that all visual artists would create carvings of their chosen tree from tree silhouettes that were sized in relation to each other. A similarity in style allows the prints to be exhibited next to each other with a unified aesthetic, and maximizes the viewers' ability to distinguish differences in size, form, and branch number between the different trees. We felt this was an important aesthetic choice.

Impact

The art making process connects people to the environment in a powerful and emotional way. Through an anonymous closed-ended survey administered by Harrower at the end of the event, and online to other participants, all collaborators ($n = 51$) strongly agreed that the art making process was more important for building emotional attachment to the science, than the importance of creating a finished artwork. Ninety percent of collaborators felt an enhanced emotional connection and personal responsibility to the issue of biodiversity loss than they had before working on this project. Eighty-two percent of collaborators reported that participation in this art–science project had inspired them to reconsider ways that their behavior negatively impacted the environment, and to make modifications. All participants surveyed felt that an in-depth science description, given both in written form and as a verbal talk, was very important to enhancing their understanding about the system, leading to an enhanced ability to make art. All participants agreed that participation in this art–science project provided them with a deeper understanding and appreciation for current issues surrounding biodiversity loss and climate change, as well as appreciation for the science process.

Cascading impacts

This project will continue to grow. As of April, 2018, the social media site is not yet open to public interaction, but once in place, viewers will be able to post directly to tree profiles by submitting letters and art. We will show the art in conjunction with science talks, a printmaking workshop at the JTNP visitors center art gallery, at art galleries, and museum exhibitions. In March 2019, as part of the art residency, we will be working with elementary school students to collect data on the trees. Participating students will create their own Joshua tree art and writings. This work has already inspired a ranger at Indiana Dunes National Lakeshore to begin plans for a local tree-dating project.

Discussion

Scientists who seek to have broader impacts, to influence the public's engagement and behavior can benefit from collaborations with artists whose creative expressions reach audiences, often evoking an emotional response. Emotions are increasingly credited with playing a central role in the decisions we make and the information we take in (Jacobson et al. 2007). In Harrower's case studies, we found that art has the potential to evoke a strong emotional response that could inspire new behaviors. As these projects are recent and ongoing, we have yet to follow up with respondents to gather evidence of long-term changes in beliefs or behavior. If the art making experience effects a strong emotional connection, it could potentially influence a person's values and habits (Matarasso 1997; Jackson 2005; Curtis 2017).

Successful collaborations require strategies that enable us to connect with collaborators, collaborate successfully, and create meaningful science inspired art works that connect with the intended audience (Nielsen-Pincus et al. 2007; Glinkowski and Bamford 2009). Harrower has tapped into opportunities for collaboration that are widely available to grad students or professors associated with a university: collaborations with art faculty, leveraging video, and social media to promote broad exposure. Interdisciplinary collaborations have shaped her outreach efforts, and the message about Joshua tree decline and species loss has taken a different form in each project. With artists' input, each of these interdisciplinary projects has given the research and topic of species loss a visual form, reaching new audiences. Interdisciplinary collaborations are recognized as an important approach to address complex environmental problems (Daily and Ehrlich 1999; Newbold et al. 2015; Frodeman et al. 2017). How those interdisciplinary partnerships are nurtured affects the product and the experience for collaborators—is the project ultimately rewarding, inspiring, or draining or even worse, embarrassing? Art–science collaborations have to wrestle with articulating an appropriate level of autonomy to artists and maintaining scientist's engagement. Extrapolating from the projects Harrower has initiated and co-led, a variety of strategies can set a project on a path to positive cascading impacts, such as treating artists as a primary audience; seeking input from public audiences; structuring public events that offer a combination of science talks and art experiences; working with a theme such as species loss as well as specifics of a scientific investigation. Cascading impacts can be achieved when a scientist integrates multiple dimensions of their identity into their professional life (Risien and Storksdieck 2018).

The cases described above illustrate how vital it is to treat artist collaborators as a primary audience for increasing knowledge, not as a necessary steppingstone to the true target audience. Time spent for knowledge sharing between disciplines is important, as a basis for building mutual respect, a sense of joint ownership, generating empathy and interdependence (Steinheider and Legrady 2004; deLahunta 2006; Glinkowski and Bamford 2009; Curtis et al. 2014). Harrower's strategic moves of involving the artists in shaping the message and elevating that message from specific details about her study to larger social implications have allowed her artist collaborators autonomy of task, team, time, and technique within the parameters of rigorous science and agreed upon aesthetics. This approach sets the stage for greater buy-in and high levels of intrinsic motivation according to research (Glinkowski and Bamford 2009; Pink 2011; Curtis et al. 2014).

Harrower and her collaborators found that utilizing conceptual models and focal themes to highlight the science issues served as an important communication device for teams to break down language barriers and frame complex interdisciplinary problems. Identifying language commonalities, metaphors, and drawing diagrams to communicate the vision greatly facilitated the process. This agrees with other work that found conceptual models to be a valuable tool for bypassing jargon and sharing knowledge between disciplines (Heemskerk et al. 2003; Frodeman et al. 2017).

In Seeking Symbiosis, Joshua tree love story, and Hey Jtree, Harrower found that collaborators reported valuing the opportunity to understand the science deeply. Unanimously, all recruited completed the projects and demonstrated a high level of investment, were personally moved to examine habits, and reported high levels of interest in further art–science collaborations. Survey data from Harrower's projects support findings from other studies describing the outcomes of successful art–science collaborations in which time invested in the artists education about the science research both enhances the artistic outcome and feeling of mutual respect for different research methodologies (Glinkowski and Bamford 2009; Miller 2014).

Across Harrower's work, all collaborators reported an enhanced connection to the science process and an increase in their emotional response to species loss that was gained through the art making process. Rather than rotely fulfilling an obligation, they became conversant in symbiotic relationships, mycorrhizal fungal networks, and aspects of phenology. This finding agrees with other work that has demonstrated group art making experiences have the potential to alter people's attitudes and beliefs (Jackson 2005; Glinkowski and Bamford 2009; Ballengée 2015). The process of research, creation, and self-reflection inherent to the art making process can assist with knowledge and identity building (Harrison and Harrison 1993; Curtis 2017).

Seeking input from public audiences through surveys and focus group discussion, Harrower keyed in to the value of pairing her science talks with artistic media. Audience feedback is an often overlooked component during the art making process (Glinkowski and Bamford 2009), but to maximize emotional impact, we found it useful. Audience feedback on a version of the animated film helped the team clarify central ideas/concepts. Scientists who have an interest in outreach and advocacy could benefit from asking an audience for feedback on a talk or art–science collaboration. To best prepare and develop materials for a diverse public, researchers could take special note on questions and comments to better understand audience's prior knowledge and areas of interest.

We found that the emotional impact of the art making process (across all three case studies) and the art viewing process (Joshua tree love story) was strongest when paired with a science talk. This finding aligns with the theory of using multiple modalities to influence knowledge acquisition, which could lead to personal changes in attitudes and beliefs (Jackson 2005). Pairing a science talk and art will be part of our way of working in the future. We can use audience feedback to determine what the advantages and disadvantages are to leading with the art experience or the science talk, as well as to determine how the audience responds if the talk is given by a participating artist or the scientist. This fusion may be a new take on science cafes, a format that opens up new venues for discussion about science and society.

As a final note, Harrower's impulse to initiate outreach projects early on in a study is somewhat unconventional. While scientists might wonder about the value of talking about their research before results are in, Harrower has found that the outreach and research efforts nourish each other. Securing funding and accessing residencies all lend credibility and support to both the research and outreach efforts.

Harrower will continue to investigate Joshua tree ecology at her research sites, assess the impact on stewardship and perceptions of beauty, urgency, as well as understanding of species interactions among her target audiences—those who are involved as citizen artists, professional artist collaborators, or public audiences in park settings and beyond. With partners from informal education, Harrower will explore how artists who have a high level of science understanding function might participate, lead, or facilitate in-person presentations paired with art exhibits or film screenings or citizen art workshops.

As evidenced by our current environmental state, we cannot assume resilience of species and their habitats. To secure a sustainable future we need to develop collaborative interdisciplinary approaches that engage the public and motivate people to protect our resources. The potential for social change through art/science goes far beyond translating science for public consumption. By forming intentional art/science collaborations like the ones described above, scientific researchers have the potential to turn information into inspiration for further learning and action to support species conservation and sustainable approaches to life on our planet.

Acknowledgments

We would like to thank Greg Gilbert, and Brent Haddad for comments on early versions of this manuscript. We thank our many arts and science collaborators who participated in the different case studies, and the supportive staff from Joshua Tree National Park for their help with fieldwork and educational outreach. We would also like to give thanks for the financial support from OpenLab, iSWOOP, SymbioStudio, and the Norris Center for Natural History.

References

A'Bear L, Hayward JC, Root-Bernstein M. 2017. Conservation science and contemporary art. Leonardo 50:27–30.

Ballengée B. 2015. Ecological understanding through transdisciplinary art and participatory biology [dissertation]: Plymoth University.

Belfiore E, Bennett O. 2006. Rethinking the social impact of the arts: a critical-historical review. Centre for Cultural Policy Studies, University of Warwick.

Bronstein LR. 2003. A model for interdisciplinary collaboration. Soc Work 48:297–306.

Carlson A. 2000. Aesthetics and the environment. the appreciation of nature, art and architecture. New York (NY): Routledge.

Curtis D. 2017. Building sustainability with the arts. In: Building sustainability with the arts: proceedings of the 2nd national EcoArts Australis Conference. Cambridge Scholars Publishing. p. 3.

Curtis DJ, Reid N, Reeve I. 2014. Towards ecological sustainability: observations on the role of the arts. S. A.P. I. E.N. S., Surveys and Perspectives Integrating Environment and Society.

Daily GC, Ehrlich PR. 1999. Managing earth's ecosystems: an interdisciplinary challenge. Ecosystems 2:277–80.

deLahunta S. 2006. Willing conversations: the process of being between. Leonardo 39:479–81.

Frodeman R, Klein, JT Pacheco RCDS. 2017. The Oxford handbook of interdisciplinarity. Oxford University Press.

Gablik S. 1991. The reenchantment of art. New York (NY): Thames and Hudson.

Glinkowski P, Bamford A. 2009. Insight and exchange: an evaluation of the Wellcome Trust's Sciart programme. London: Wellcome Trust.

Harrison HM, Harrison N. 1993. Shifting positions toward the earth: art and environmental awareness. Leonardo 26:371–7.

Heemskerk M, Wilson K, Pavao-Zuckerman M. 2003. Conceptual models as tools for communication across disciplines. Conserv Ecol 7:8.

Jackson T. 2005. Motivating sustainable consumption. Sustain Dev Res Netw 29:30.

Jacobson SK, Mcduff MD, Monroe MC. 2007. Promoting conservation through the arts: outreach for hearts and minds. Conserv Biol 21:7–10.

Kay A. 2000. Art and community development: the role the arts have in regenerating communities. Community Dev J 35:414–24.

Mason J. 2017. Qualitative researching. London: Sage.

Matarasso F. 1997. Use or ornament. The social impact of participation in the arts. London: Comedia/Arts Council. p. 4.

McKibben B. 2011. Eaarth: making a life on a tough new planet. Canada: Vintage Books.

Miller AI. 2014. Colliding worlds: how cutting-edge science is redefining contemporary art. WW Norton & Company.

Neff M, Sumner D, Bawden GW, Bromberg E, Crutchfield JP, Davidson D, Gilbride S, Kellogg LH, Kreylos O. 2010. Blending art and science: collapse (suddenly falling down). Leonardo 43:274–81.

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Nielsen-Pincus M, Morse WC, Force JE, Wulfhorst J. 2007. Bridges and barriers to developing and conducting interdisciplinary graduate–student team research. Ecol Soc 12: 8.

Novacek MJ. 2008. Engaging the public in biodiversity issues. Proc Natl Acad Sci U S A 105:11571–8.

Pink DH. 2011. Drive: the surprising truth about what motivates us. Penguin.

Risien J, Storksdieck M. 2018. Unveiling impact identities: a path for connecting science and society. Integr Comp Biol. (doi: 10.1093/icb/icy011).

Steinheider B, Legrady G. 2004. Interdisciplinary collaboration in digital media arts: a psychological perspective on the production process. Leonardo 37:315–21.

Winfree RA, Dunaway F. 2011. The nature of art: communicating park science, nature and culture through art. Alaska Park Sci 10:53–63.

Integrative and Comparative Biology
Integrative and Comparative Biology, volume 58, number 1, pp. 113–126
doi:10.1093/icb/icy033
Society for Integrative and Comparative Biology

SYMPOSIUM

Designing for Broad Understanding of Science Insights from Practice

Nickolay Hristov,[1,*,†] Carol Strohecker,[‡] Louise Allen[†] and Martha Merson[§]

*Center for Design Innovation, 450 Design Avenue, Winston-Salem, NC 27101, USA; †Winston-Salem State University, Winston-Salem, NC 27110, USA; ‡College of Design, University of Minnesota, Minneapolis, MN 55455, USA; §TERC, Cambridge, MA 02140, USA

From the symposium "Science in the Public Eye: Leveraging Partnerships" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1] E-mail: hristovn@cdiunc.org

Synopsis With the acceleration and increasing complexity of macro-scale problems such as climate change, the need for scientists to ensure that their work is understood has become urgent. As citizens and recipients of public funds for research, scientists have an obligation to communicate their findings in ways many people can understand. However, developing translations that are broadly accessible without being "dumbed down" can be challenging. Fortunately, tenets of visual literacy, combined with narrative methods, can help to convey scientific knowledge with fidelity, while sustaining viewers' interest. Here we outline strategies for such translating, with an emphasis on visual approaches. Among the examples is an innovative, National Science Foundation-funded professional development initiative in which National Park rangers use scientists' imagery to create compelling explanations for the visiting public. Thoughtful visualizations based on interpretive images, motion pictures, 3D animations and augmented, immersive experiences complement the impact of the natural resource and enhance the role of the park ranger. The visualizations become scaffolds for participatory exchanges in which the ranger transcends the traditional roles of information-holder and presenter, to facilitate provocative conversations that provide members of the public with enjoyable experiences and well-founded bases for reflection and ultimately understanding. The process of generating the supporting visualizations benefits from partnerships with design professionals, who develop opportunities for engaging the public by translating important scientific findings and messages in compelling and memorable ways.

Introduction

Scientists are not strangers to the power of visuals to communicate, illustrate, and further their own thinking. One can trace this theme across time and place, from Galileo and Darwin to Einstein and Feynman (Feynman 1995; Laiser 2005; Tufte 2006). Scientists' visual material has the potential to foster the public's scientific literacy, especially when intermediaries like park rangers and museum educators incorporate such material into a larger narrative or inquiry-based experience. Live interpretation can generate interest, increase understanding, and be a catalyst for conversations about scientific process as well as the relevance of research (Marino and Koke 2003). All visuals are not equally suitable for the purpose of increasing scientific literacy, however. For example, the visual material scientists collect and produce may be immediately eye-catching and appealing or not. In this paper, we describe the characteristics of visual material that in the hands of a skilled presenter can accomplish one of three goals: captivate interest; enhance the public's understanding of a breathtaking resource by illustrating hard-to-grasp concepts; and spark conversations about the value or relevance of scientific research. To do this, we discuss design principles and their application in several parks participating in the project, Interpreters and Scientists Working on our Parks (iSWOOP, National Science Foundation [NSF] DRL-1514776). iSWOOP makes park-based research an interactive part of the visitor experience at national park sites through the use of imagery generated by scientists conducting on-site

Advance Access publication June 4, 2018

research. This approach relies on and extends the visual literacy, as well as the scientific literacy, of all partners.

Background and definitions

"Imagery," "scientific illustration," "visualizations," "representations": these terms have proliferated, but they leave us with an imprecise vocabulary both for referring generically to 2D visual material and for distinguishing among different types of such imagery. Rooted in the history and tradition of data science, the word "visualization" evokes displays of large, complex data sets, collected with expensive instrumentation through multi-year efforts with contributions from expert scientists, analysts, programmers, and designers—whereas "image" has the connotation of immediacy or direct translation from 3D to 2D, as with photography. However, the prevalence of photos in our culture and the ease with which anyone can generate these images obscure the effort that can go into composing and editing photos. Such ambiguities complicate provision of guidance for scientists striving to communicate their work to the general public through reliance on visual modalities.

By the terms noted here, we collectively reference the variety of visual representations scientists use to document phenomena, represent meaningful observations or trends, and model how things work. By "images," we mean to encompass a variety of visual material that could be compiled in a visual library, a trove of visual resources for educational use. Photographs arranged to suggest a comparison, animations to show a sequence unfolding in time, or data visualizations to assist understanding of complex cause-and-effect relationships are all visual material that park rangers and docents can draw upon in their work with the public. In this article, we want to be inclusive and suggest that intermediaries in partnerships with scientists consider all manner of visual material, including photographs, maps layered with text or other augmentations, illustrations, infographics, time-based representations like slide presentations and video, three- and four-dimensional representations, and *n*-dimensional experiences like simulations and mixed-reality environments.

Visual literacy spans a variety of fields, including art and politics as well as science. Most definitions focus on the ability to make meaning from signs and symbols. The term "visual literacy" was first coined in 1969 by John Debes, a prominent member of the International Visual Literacy Association (IVLA).

> Visual Literacy refers to a group of vision-competencies a human being can develop by seeing and at the same time having and integrating other sensory experiences. . . . When developed, they enable a visually literate person to discriminate and interpret the visible actions, objects, symbols, natural or man-made, that he encounters in his environment. Through the creative use of these competencies, he is able to communicate with others.
>
> IVLA.org and Univ. of Maryland. http://www.humanities.umd.edu/vislit/basics.php.

This definition is particularly useful because it acknowledges input from sensory experiences beyond the visual. Including sound and tactile input makes sense for educators working in natural settings.

A more recent definition proposed by those active in the field emphasizes purposeful applications for visual literacy. The visually literate advance thinking and decision-making (North Central Region Education Lab and the Metiri Group 2003) and are "competent contributor(s) to a body of shared knowledge and culture" (Association of College and Research Librarians, ACRL, 2011). Definitions of and standards for visual literacy are increasingly expansive, including understanding ethical and legal issues associated with visual material (ACRL, 2011).

Secondary and higher-educated students are not necessarily prepared to express themselves visually, make effective arguments with visuals, and coordinate visuals with other information (Green 2006). Educational researchers have found that some students tend to exhibit less comfort and skill with observing, interpreting, and discussing visual information than they do with textual information, and do so with less specificity (Hattwig et al. 2013). Clearly one cannot take visual literacy for granted. Media experts note that both the content and the composition of an image influence meaning-making; different individuals will read the same image in different ways depending on their knowledge, skill, experience, beliefs, and values; and the "constructedness" of all media messages is not necessarily obvious to all audiences (Jarman et al. 2012). Media experts recommended not glossing over basic ideas, such as: (1) photographs are not simply "records of reality"; at both capture and editing stage, they are manipulated; (2) graphs may oversimplify relationships and imply certainty; and (3) invisible objects or phenomena may be "lent" the optical properties of familiar objects (Jarman et al. 2012).

Visualization spectrum

In recent years, data have become increasingly easy to access through widespread devices such as pocket-sized cameras and cell phones. In tandem, an

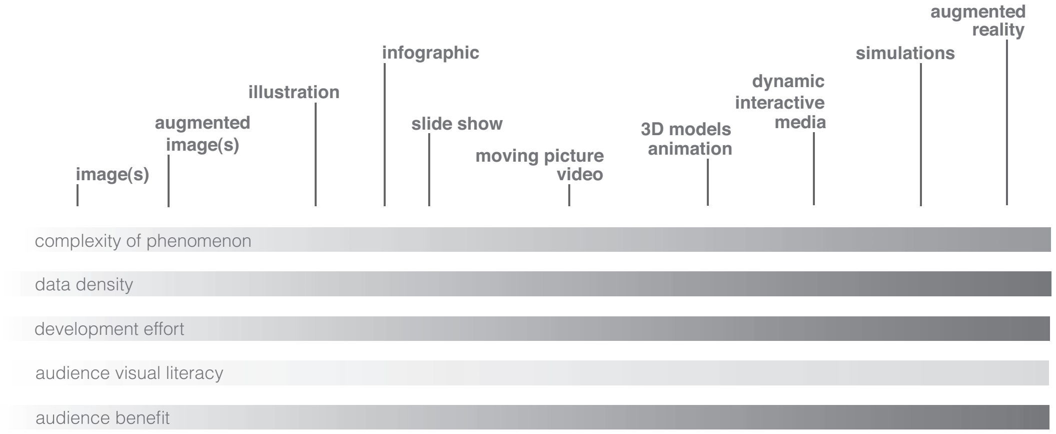


Fig. 1 Spectrum of visualizations showing visual forms and associated gradients, from low to high, that influence the development and interpretation of each form.

increasingly large and wide array of visual expressions heightens demand for viewers' time and attention in a busy visual world. In our work with the iSWOOP initiative, we recognize that visualizations are becoming increasingly demystified and accessible visual expressions previously reserved for the domains of experts. We contend, further, that intensely informative visual constructs can be created across a range of image types (Fig. 1): visual expressions may include photographs, images layered with text or other augmentations, illustrations, infographics, time-based representations, such as slide presentations and video, three- and four-dimensional representations, and *n*-dimensional experiences like simulations and mixed-reality environments. Discerning the appropriate expressive vehicle for a given communication need is part of the design process.

Further defining this spectrum of visualization types are dimensions such as: data density and complexity; development effort, acknowledging the often multi-phased workflows and handoffs needed in realizing captured data as a visual image; and less commonly shared concepts such as audience benefit and presumed visual literacy. Other dimensions are not yet represented in this spectrum, such as the fine-grained attributes of range of quality in artistic rendition and degree of interpretation vs. exact empirical representation. Nevertheless, the spectrum as currently articulated may aid decision-making about which visualization type to choose for a particular application. Communicators should carefully consider pros and cons of the overall development effort, accuracy and richness of content representation, and audience experience and benefit. When visualizations are candidates for revision or for scaffolding, design partners are invaluable. Their skillful eye and understanding of synthesis can help marry the purpose and the presentation.

Visual augmentation in park settings

Museums, parks, science centers, and aquarium facilities share attributes such as intergenerational audiences of choice and learning opportunities without traditional accountability measures. Exhibits and live interpretation are on offer. But among informal learning institutions, there are differences as well. Park visitors might stay for days, taking advantage of multiple opportunities for ranger-led science learning experiences. Recreational activities like kayaking and rock-climbing on protected lands offer opportunities that both enhance and distract from STEM learning. The public's attention span varies widely and, especially in parks, the duration and location for interpreters' use of a visual library with material contributed by scientists must factor into design decisions. Parks are an opportunity to get away from screens, yet digital imagery has the potential to reveal non-visible aspects of a place and arouse visitors' curiosity (Zimmerman and Land 2014). Well-chosen images can illustrate concepts particular to scientific disciplines, amplify visitors' observations, and encourage deliberate comparisons of natural structures or conditions (Zimmerman and Land 2014). Images that reveal something unusual about the park resource can engage visitors, causing them to stay with an interpretive interaction longer (Metros 2008; MacArthur 2014; Merson et al. 2016).

Related to live interpretation, we have adopted an approach we call visual augmentation (ViA). ViA is a design style that deliberately accommodates a range of visual formats, leaves space for audience involvement, and is adaptable for rangers to shape story lines and guide interpretive conversations. ViA stands in contrast to modalities such as the science poster, concept map, or traditional infographic, which provide all the necessary information and notations for the viewer to interpret the content without a presenter. ViA material purposefully leaves room for a presenter, a facilitator, or interpreter to steer the conversation and cultivate a meaningful learning experience in response to conditions of a given moment. The goal of ViA is not solely to inform, but rather to engage. Such material does not contain all information needed for interpretation; instead, it provides a visual point of departure and relies on the facilitator or storyteller to craft a story or learning experience that is further enriched by visitors' questions, past experiences, and reactions. That is not to suggest that ViA content is incomplete; rather, it is deliberately minimal.

Ambiguous images may have the effect of enticing visitors to wonder or ask for more information. Constructivist math educators explain how images with only simple labels or without summary statements can engage a viewer so as to support the self-construction of meaning. Presenting graphs as composite images that successively augment the positions of charted data can also promote learning (Nemirovsky and Noble 1997). Sensitive treatment of graphs is especially important, given the general usefulness of this visual device in representing scientific information and the finding that a learner ascribing meaning to data depicted in a graph is taking a crucial first step toward finding relevance in the phenomenon being represented (Russell and Corwin 1989). The versatility of data visualizations makes them a powerful component of a visual storyteller's repertoire: visualizations can express a disturbing or hopeful trend; they can function as the entire message or the moral of a story, as punch line or wake-up call (Ham 1992, 21).

Below we describe in more detail the design principles that characterize ViA material, its development and use, bridging theory, and practice.

Design principles

Designing visual material for most scientists is an exercise in communicating with peers through posters or PowerPoint presentations, rather than products for public audiences. In our own efforts to navigate this space, we had a number of epiphanies and realized in successive revisions that:

(1) Juxtaposed images or video clips were more helpful for inviting observations than a single image.

(2) A complicated graph might be a turn-off, but with a sequence that moved from a simplified to complex version (scaffolding) and a story about collecting the data, presenters could use a graph as the centerpiece of a conversation with a park visitor and propel the dialog toward seeing patterns and making predictions.

(3) Images of the life stages of a charismatic species could evoke questions that would lead to discussing research challenges and the inevitable revisions and refinements that are part of scientific process.

In conversing with scientists beyond our project group, we realized that we needed a language for the ViA style. We needed to articulate principles to guide composing visual material, for a public audience in a setting that promotes informal learning. Without these principles, it was easy to default to the most familiar formats and conventions. For example, PowerPoint slides are often a photo next to bulleted text. Graphs for scientific publications tend to have unfamiliar unit labels and display multiple kinds of data, such that they are most accessible to peers immersed in similar work. Illustrations of science concepts often have a cartoon-like style with labels and arrows. We rejected this style as it evokes associations with school, inappropriate to the free-choice, out-of-school learning environment. Instead, we borrow and build upon influences from fields of design.

To help guide the development and use of visually represented content, we urge partnerships with designers. To facilitate communication among cross-disciplinary partners, we identify six design principles. Lists of foundational design principles abound. Clearly there is a craft to learn and though fundamental principles are helpful, they are like mere grammar pointers, which do not necessarily result in persuasive writing. We recognize and readily admit that our ViA principles are not fundamentally new formulations; instead, they are a compilation and extensions of existing good-practices and expert-recommendations from the fields of graphic design, marketing, data visualization, and statistical science (Wong 1972, 1977, 1993; Dondis 1973; Tufte 1990, 1997, 2001, 2003, 2006; Doumont 2002, 2005; Duarte 2008; Gross and Harmon 2009). Our contribution is in distilling the adages most applicable to science translation and supplying examples from a science-based, informal STEM learning project on protected lands. We include recommendations for future use of these principles, specific to science communication in the ViA style. ViA visualizations tend to be cinematic,

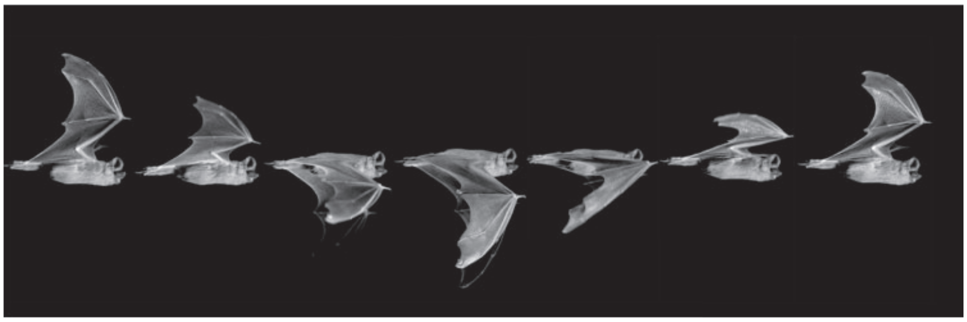


Fig. 2 Stages in the wingbeat cycle of a flying Brazilian free-tailed bat derived from high-speed videography and showing details of the movement not discernible with a naked eye.

minimally labeled, design-informed, narrative-driven, multi-modal, visually impactful, and thought-provoking. In the spirit of Edward Tufte's critique (2003), bullet points are taboo. Labels, legends, and references are carefully considered based on the intended use and particulars of the visitor experience.

The iSWOOP project—a case study for visual communication

Examples from a science-based informal learning project on protected lands emerged from a collaboration among wildlife biologists, park-permitted scientists, park rangers, informal education researchers, and designers. The National Science Foundation-funded model for innovative professional development of interpretive park rangers at America's national parks, Interpreters and Scientists Working on Our Parks (iSWOOP), has been the impetus for convening an interdisciplinary team. NSF, iSWOOP, its park, and scientist partners all recognize that for millions of visitors the many park-based and park-relevant science projects are invisible—happening behind the scenes, away from the public eye—constituting a missed opportunity to showcase scientific research. (The professional development model is described elsewhere in this volume by Allen et al. 2018.)

To bring these stories and experiences to the public eye, mixed-media artists, illustrators, graphic designers, 3D animators, film editors, data analysts, and computer programmers work in close consultation with educators and featured scientists to craft libraries of visual material (visualizations) that feed memorable visual stories and learning experiences. iSWOOP's Visualization Team relies on feedback from park rangers and advice from informal educators. Rangers make sure that visualizations augment rather than conflict with the awe-inspiring experience of the natural resource. All contribute to the iterative process of crafting stories through which members of the visiting public further their understanding of science. (Benefits for scientists are described elsewhere in this volume by Allen et al. 2018.)

Equipped with excellent storytelling skills, interpretive park rangers are ideal ambassadors for the science messages that often get left out of the public discourse. In park rangers' hands at iconic, culturally or naturally significant locations, rangers are conduits for science, conveying how we know what we know; stories and experiences behind the science; the layered process of discovery, checkered with moments of successes and often of failure; the importance of questioning and revising; and ultimately relevance to people of diverse backgrounds and broad interests (Merson et al. 2018).

The iSWOOP project dovetails well with park rangers' mission to nurture emotional and intellectual connections between the visitors and the cultural and natural resources (Ham 1992).

Example 1 (Fig. 2): Instead of answering directly a visitor's question about how bats fly, an interpreter at Carlsbad Caverns (CAVE) National Park shows a slow-motion video of a flying Mexican free-tailed bat. Visitors are invited to observe details of the movement not seen with the naked eye, ponder how the images were taken, and speculate about the mechanism of the flying creature, as the ranger carefully facilitates the conversation.

Example 2: A park ranger shares thermal video of the bat roost, with no access for the public and highly limited access for staff. The videos provided by permitted researchers serve as a catalyst for insightful conversations about the motivating questions, data recording and rendering techniques, and challenges of the research program.

Through the expansion of such methods at five National Parks across the United States, thousands of park visitors are now learning first-hand about on-site science. At CAVE, they see cutting-edge research with thermography of bats and laser scanning to enable surveying the cave and mapping its morphology; at Acadia (ACAD), visitors consider changes in landscape and succession of plant communities since the last glacial maximum; at Indiana Dunes (INDU), visitors ponder wetland ecology; at Joshua Tree (JOTR), they learn about botany; and at Jean Lafitte (JELA), visitors consider the migratory biology of the Prothonotary Warbler (or swamp canary). Visitors engage in conversations and share in visual experiences that deepen the impact of park visits and create reasons for long-term connection with the natural resources (Merson et al. 2017).

This essence of the iSWOOP model is both scalable and adaptable to the range of science found at varied sites of public engagement. Here we share some of what we have learned through iSWOOP, hoping that our pursuits will prove useful to SICB's scientific community. We also aim beyond this immediate audience, recognizing that many similar partnerships are needed to effect broad understanding of science in contemporary culture.

Applying the design principles

As mentioned above, ViA Design Principles are a compilation of existing good-practices and expert-recommendations from the fields of graphic design (including print and web), marketing, data visualization, and statistical science (Wong 1972, 1977, 1993; Dondis 1973; Tufte 1990, 1997, 2001, 2003, 2006; Duarte 2008). Our contribution is in distilling these adages into a style-set, with examples from practice and recommendations for future use specific to science communication in the ViA style.

Design principle 1—narrative

Foremost in the development of ViA material is the presence of a *narrative* core around which visualizations and their interpretations are built. The potential for a narrative anchors the overall approach to communicate the scientific content and to establish an intellectual as well as an emotional connection with the audience. By invoking narrative as a design principle, we accept the arc of the novel, drama, or short story as a template for organizing information. A narrative includes: setting, characters, conflict, events building to a climax, and a conclusion. In other cultures, stories of origin, fables, and teaching tales culminate in a moral. Archetypal conflicts are centuries-old formats for relaying events that happen to a featured character—either unexpected connections, a struggle between good and evil, or an unanticipated break-through, which lead to events with broader implications.

A growing and increasingly accepted body of work indicates that audiences find narrative-based science communication easier to understand and more engaging than logic-based science messages. Furthermore, narrative processing is more efficient and associated with increased recall, ease of comprehension, and shorter reading times (Schank and Abelson 1995; Zabrucky and Moore 1999). This categorical distinction may stem from the apparently special status of narrative structures in human cognition (Graesser and Ottati 1995). It is also well established that narratives are inherently persuasive and, because they communicate content from the perspective of a particular experience rather than logic-deduced truths, they have no need to justify the accuracy of their claims and thus can perpetuate misinformation (Dahlstrom 2014). Nevertheless, a strong narrative structure gives rise to a vivid, memorable experience. Details packaged in a story can easily be summoned and retold and, because of the empathy that they cultivate, stories with strong narrative structures can become prominent in individuals' relational repertoires (Zimmer 2018). The consensus in the field of narrative research is that such an approach to science communication for non-expert audiences is a potent and promising tool when applied sensibly and ethically (Nathanson 2006). The importance of narrative structure in conveying scientific information to diverse, non-expert audiences has been popularized by Randy Olson (2009, 2015).

iSWOOP visual materials are compiled in a Visual Library, available to rangers who create their own programs and sequences. There is no single script or story. Because the interpreters flexibly include audience members in the telling of any given story, iSWOOP guards against the largest of narrative pitfalls—the propagation of a single point of view (Adichie 2009). iSWOOP, through ViA, inherently invites plurality.

Consider the following example from a park ranger program at INDU National Lakeshore (Fig. 3): In discussing wetlands as a diverse, underappreciated and threatened resource, park rangers at INDU point out that the Grand Kankakee Marsh, once called the Everglades of the North, covered more than a million acres across north Indiana and parts of Illinois as recently as the mid-19th century. By the 1950s, more than 95% of the area of that wetland complex was lost due to draining, agriculture, and development, with profound effect on the hydrology, ecosystems, biodiversity, and economy of the region. The ranger could easily cite the statistic and move on. Instead, s/he sets a narrative in motion. She asks participants to imagine their dream house. They shout out its attributes: a

Fig. 3 Narrative approaches give a personal context and point of reflection for public audiences when presented with the history of the Grand Kankakee Marsh (**A**), once a mighty wetland complex that has been reduced to less than 5% of its original size ((**B,C**) see text for details).

fireplace, a large kitchen, a swimming pool. She pauses and tells participants that she is taking away their favorite parts. The ranger displays a digital composition showing the layout of a 2000 square-foot house plan on a tablet. In a series of steps, the ranger then omits sections of the floor plan until the same 95% of the original floorplan is gone, leaving only critically selected sections like the bathroom and kitchen pantry. The sense of loss is palpable. The ranger reminds participants of the extent of the Big Marsh—once home to many species—and without saying much more, the participants relate, feeling the impact of the loss of the Grand Kankakee Marsh as a living space.

Design principle 2—functional minimalism

While the first design principle, Narrative, relates to ViA's commitment to live interpretation, functional minimalism exerts a prominent influence on its visual style. The goal is to distill the visual composition to include the most important visual elements. We strive to design minimal, "clean" visual translations that prompt curiosity and facilitate thoughtful conversations, creating space for guided interpretation or the viewer's own discovery and construction of meaning. Thus, if a visual element is used, then it has a purpose and meaning (e.g., if there are red and blue elements in the composition, then we assume that color has a meaning). Decorative use of color or line is not advisable because such additions risk distraction, at best, and misinterpretation, at worst (Wong 1993; Tufte 2006; Duarte 2008; Fig. 4).

The introduction of any elements and stylistic treatments should serve a purpose in the composition. For example, if two images, graphs, or other visual features are presented simultaneously in the same composition, then we infer that the viewer should engage in side-by-side comparison. Understanding through comparing and contrasting the material justifies the simultaneous presentation. Otherwise, these elements should be presented sequentially and the viewer should be invited to follow the narrative in developing a progressively increasing understanding of the topic.

Design principle 3—compositional prominence and impact

ViA authors place elements in a spatial arrangement and hierarchical organization to correspond to their role in the visual narrative. This design principle reinforces the notion that size and spacing in visual composition matter (Dondis 1973). In the case of photographs or videos, important compositional elements should occupy a large portion of the entire canvas. Image elements should include sufficient resolution and detail to allow observations, interpretations, and reflection. Too often, driven by generic software templates, visual compositions include many images and visual elements clustered in the same frame. While functional minimalism dictates that such treatments should be avoided, here we further suggest that visual authors should strive for hierarchical organization, giving important elements larger portions of the canvas. Secondary and associated relationships with other elements should be communicated via relative size, scale, placement, and proximity. Multiple elements should be "spread over" several frames into a logical sequence (see next section). Similar attention should be given to the presentation environment as well. Too often, months if not years of data collection, analysis and design work are compromised by the size of the presentation screen, the poster guidelines, or the resolution of a handheld digital tablet. Without testing on the actual display device that will deliver the content to the public, carefully composed visuals end up as content that is difficult to understand.

Fig. 4 Minimally designed visualization that compares a toad and a frog by inviting the audience to discover on their own the characteristics of each species (**A**). (**B**) offers a different approach (see text for details).

Design principle 4—flow, sequence, and continuity

Compositional flow

Flow is about movement and direction, leading the eye from one part of a composition to another according to the author's intentions. Even static compositions can impart a visual flow—it is created through a combination of the placement of visual elements and their corresponding weight and visual direction. Elements of greater visual weight serve as focal points, pulling the eye and defining resting places. Other elements impart direction, moving the eye from one point to another through such overtly visual cues as arrows and lines, or more subtly through echoes of color or shape. The result is an intuitive movement through the composition, the eye, and mind working in concert to process the presented information quickly and efficiently. Through such considerate composition, the viewer can process dense information quickly and be ready for the next piece of information without missing important points or becoming fatigued or distracted. Such ideas are well established in marketing, web design, and compositional presentation formats. To date, however, the use of such techniques by the scientific community is limited—particularly outside of the mainstream media and publication domains, where communicating scientific content could be most impactful (Dondis 1973; Wong 1993; Tufte 2006).

Sequencing

Beyond flow within a static composition, when a ViA narrative calls for representation in the time domain (as through a slide presentation, animation, film, or video), the appearance of one image after another dictates how to construct and present the information. As Design Principle 2 applies Functional Minimalism in simplicity and efficiency to the design of compositional space, Sequencing does the same with regard to time. Good sequencing suggests a visual logic in place or time. The visual treatment paces the presentation of information, extending the story's potential from a single composition in space to a progression that plays out over time. Attention to narrative detail continues to be vitally important. Film editors compose a story with one or more acts, each of which includes several sequences. Each sequence is divided into one or more scenes. Scenes, in turn, are built out of individual shots (Gulino 2003). Similarly, in developing time-based ViA content, the point is not simply to assemble pieces mechanically into a logical sequence, but to consider visual elements and compositions that inform, engage, and invite dialog about a study's conclusions and possible future scenarios. The storyteller, either park ranger or facilitator, can tell a coherent story or add a distinct perspective, and the ranger can establish a rhythm or tempo to the conversation. In film, the audience is watching; the viewer of a ViA interpretation is invited to be an active participant.

Continuity

Following closely from Sequencing, Continuity creates small-step transitions between elements in a spatial composition or temporal progression. Such transitions facilitate visual interpretation and retention of information from one time-point or compositional element to the next, making the narrative seem intuitive and easy to follow. Visual continuity supports understanding and memory at a higher cognitive level than the interpretation of speech or text alone. Thus, we argue, continuity is an important narrative element that enables the understanding of dense, layered material such as the verbal interpretations from the presenter and the visual flow on the screen (see Multimodality below). The "presentation," then, becomes less of a compilation of individual visual compositions or elements, and more of a seamless flow of content that happens to be "housed" in individual frames or presentation steps.

In the example in Fig. 5, Sequencing alone will dictate the three scales to be shown. Compositional Flow will further determine the arrangement to inform the animation of the sequence from one spatial

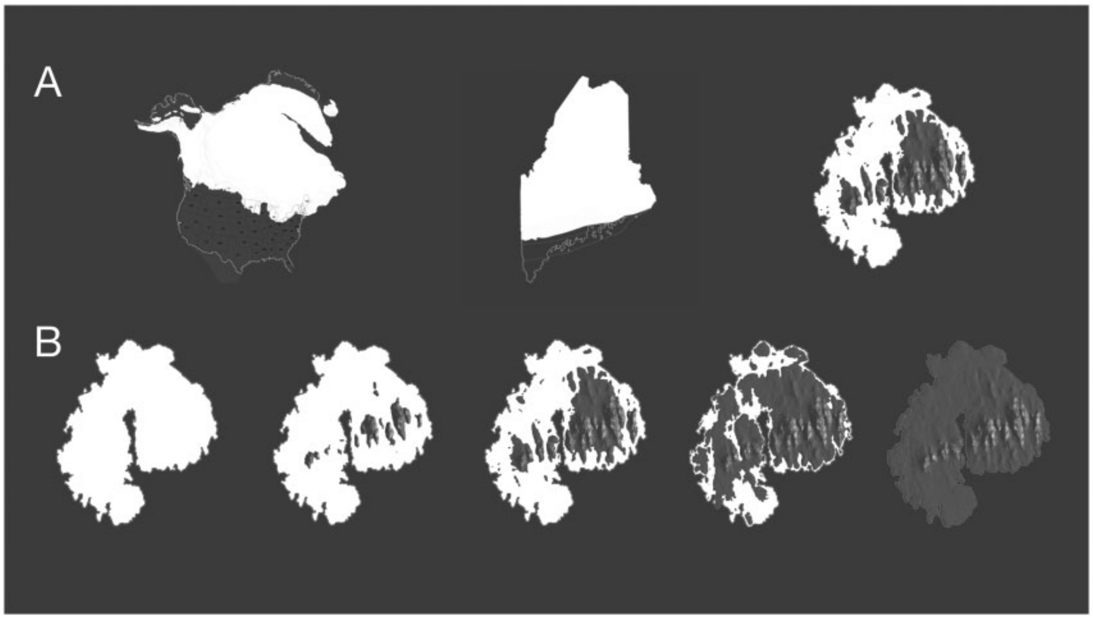


Fig. 5 A conversation about the deglaciation of the Northeastern coast of North America starts at the continental level and proceeds to the state level before arriving at the scale of Mount Desert Island (MDI) where ACAD National Park is located (**A**). Using animation, (**B**) illustrates the melting of the glacier and its effect on the landscape.

scale to the next. Visual Continuity via placement, scale, and movement communicates the relationships among the continent, the state, and the island. We assert that such a visual approach operates at a higher level than simply speech, text, or static illustration (McDougall et al. 2001). Together it is a richer, more engaging, and more efficient communication format.

For example, in Fig. 5, sequencing sets up a discussion of the effect of glaciers and deglaciation on Mount Desert Island (MDI), ME. Plate A: Interpreters seek place-based information (McFarland, November 2017, personal communication), but since the conditions on MDI were caused by changes at a continental scale, they needed a larger canvas, so to speak. One option for a narrative sequence enabled them to illustrate the glacier's continental coverage, then to zoom in on conditions in the state of Maine, and eventually to move to the scale of the island. Through this progression, the facilitators drew attention not only to the changes in ice covered land, but also to other related factors: (1) to the rebound effect once the weight of the glacier was no longer depressing the land; (2) to the coastline where the sea level advanced once the water tied up in the glacier melted; and (3) to the trees that raced to populate areas that were once ice-covered. Which plate to start with, how to intersperse the plates with information or prompts for predictions, and how much to broaden or constrain the conversation was something the park rangers experimented with. The discrete slides (vs. a pre-set animation) mean that the facilitators can be flexible and the visual material can accommodate different communication and facilitation strategies.

Design principle 5—multimodality and dynamism

Multimodality

The representation of Multimodality in communication theory is well established, describing communication in terms of textual, aural, linguistic, spatial, and visual resources—or modes—used to compose messages (Serafini 2012). Multimodal communication recognizes that a deeper informational exchange potential exists when more than one mode is invoked. Although human interaction is inherently multimodal (e.g., body language paired with voice tone and cadence), its reflection in academic and research contexts tends to be remarkably sparse in favor of a "professional" delivery that is neutral in tone and restrained in body language. In a famous critique of the visual and cognitive style of PowerPoint, Edward Tufte (2003) convincingly argues that visual noise and clutter waste the modality. Literally, countless slides are created daily around the world that feature bullet points that function as a teleprompt for the presenter to repeat out loud. Tufte similarly rails against presentation modes where small chunks of information are presented in a complicated way with the goal to push the presenter's agenda (Tufte 2003). A preferable

Fig. 6 A long color transition reveals the natural coloration of the American toad, prompting the audience to consider/reflect on the abstract representation of the B&W image and get introduced to color through an unexpectedly dynamic experience.

alternative, to better employ the phenomenal power of the projected computer screen, is to compose images that feature visual elements or data representations and use that information as anchors for building the message or interpretation.

If visual elements are carefully selected and coordinated in their presentation and interpretation, the information transfer is relegated to a different cognitive effort than conversation and verbal interpretation alone (Bearne and Wolstencroft 2007; Bhojwani et al. 2009; Serafini 2012). Discriminating use of other modalities, such as sound, tap into the richness of the communication. A short video or sound clip elicits attention from the audience. ViA's aesthetic would subtly lead up to a finale with a well-crafted visual sequence, inviting the audience to engage the information in dialog with an interpreter.

Dynamism and novelty

Dynamic content is vigorous, active, and appealing because of the rich experience it evokes. Humans are wired to detect changes: motion captures attention. Although visual dynamism can be achieved through well-sequenced and continuous material as described above, dynamism can also be generated in novel, unexpected, and subtle ways. In the world of fast-cut trailers, shaky camera YouTube videos and gimbal-stabilized fly-throughs, the absence of such intense optical overload could be equally riveting, attracting, and holding the viewer's attention if the presentation is carefully cultivated.

The opening slide of a science talk can be unexpectedly dynamic if the presenter chooses to break the banal format of a static title with author and institution layout with the inclusion of a clever moving element. A dynamic component related to the topic of the presentation can be particularly effective, such as a fluttering butterfly wing in a presentation about monarch butterflies. Even if slight, such original and thoughtful effects can catch the attention and focus anticipation of the rest of the talk. The resulting effect is more than an attention-grabbing gimmick—a presenter can use dynamism and novelty for educational benefit. iSWOOP has adopted this practice. In the instance described below, it is used along with functional minimalism to limit the distraction of color and focus the discussion on morphology.

For example, at INDU National Lakeshore, rangers introduce the question: What is the difference between a frog and a toad (Figs. 4 and 6)? Visitors examine the morphology of each pictured animal in black and white. Then, the ranger gradually over several seconds brings in the natural color of the animals. The change mid-conversation makes the image new again. The viewer makes sense of color as a layer of additional information.

Design principle 6—symbolism

Symbolism and the field of semiotics have deep roots—they are part of a diverse landscape that touches on philosophy, cognition, psychoanalysis, and culture. Guided by common symbols, we turn appliances on, activate devices we have never seen before, operate vehicles in unknown environments, and navigate mega-sized travel hubs. Viewers' recognition of signs and symbols can reduce cognitive load (Marino and Koke 2003) and accelerate appreciation of the subject. Research shows that the interpretation of symbols is not universal or 100% accurate; designers need to condition the audience, taking into account cultural norms and context (Magurno et al. 1994). Once established, however, symbols are effective at (1) facilitating memorization, (2) improving recollection, and (3) providing broad information exceeding the specific items it portrays (Vezin 1984). Furthermore, because symbols are pictorial, they take advantage of the many benefits of visual imagery: (1) since an image is processed in parallel and therefore more quickly than words, which require serial processing, identification is more precise from a single glance, at a greater distance, and at a greater speed than with words (Collins and Lerner 1982; Lehto 1992); (2) an image, memorized and recalled as a single unit, would resist interference better than a text made up of several parts. Images, therefore, have higher resistance to cognitive interference (King 1975; Santa 1977) and are perceived better in suboptimal conditions (Ells and Dewar 1979); and (3) communication with symbols and pictograms enables deeper level of processing and greater consolidation in memory due to dual

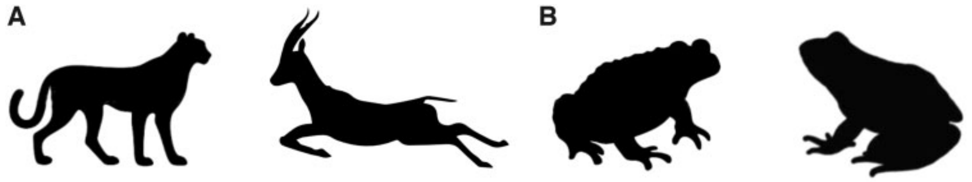


Fig. 7 Minimal symbols and silhouettes are easier to interpret and remember for the public than the elaborate coding elements and notations, typically used in scientific publications. In (**A**) the silhouettes of a cheetah and an antelope are readily recognized by even a naive audience. In (**B**) the audience will need a conditioning experience before it recognizes that these are the silhouettes of a toad and a frog. Nevertheless, once given the opportunity to make the association, the speed and accuracy of the recognition are analogous to Plate A.

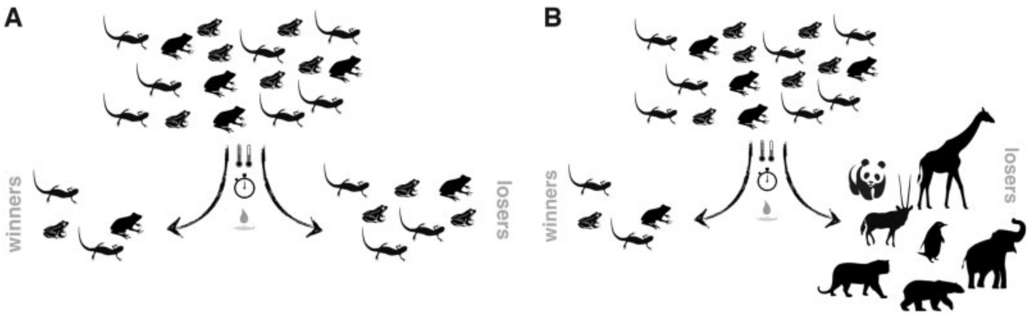


Fig. 8 (**A**) In a study at INDU National Lakeshore, simulating the effect of rising temperatures and associated climate change on 17 species of common amphibians in the park (Brodman 2009), four species are predicted to be likely survivors (i.e., winners) and seven species are likely to go extinct (i.e., losers). (**B**) A visual composition relying on minimal symbols and silhouettes for the different species elegantly takes the conversation from the territory of INDU to a philosophical discussion about ecosystems, the value of wildlife, conservation efforts, and others.

encoding that is both visual and symbolic (Paivio 1986).

We are surrounded by symbols and know how to use them. If most individuals can sit in a rental car they have never seen before and drive away within minutes because of consistent conventions and symbolic notations, why do we not use this extensive system of interacting with members of the public when attempting to communicate content that is well suited for such exchange conventions? Similarly, in a talk about predator–prey interaction—which includes a graph taken directly out of the scientific publication—why are the cheetah and the antelope represented with a solid black line and a dashed-gray line, when a silhouette of each would reproduce well in print and projection and would yield instant recognition of the creatures and their interaction (Fig. 7A)?

Going on the premise that an icon is better than a label and an image is better than text (Norman 1990), the ViA style benefits from judicious use of symbols and labels to tap into this inherent ability to utilize pictorial information. Returning to the example in Figs. 4 and 6 again, once the viewer has been introduced to the two species through the clever use of minimal design and sequenced presentation of information, in subsequent discussions any future reference to the two species can be reduced even further to the two descriptive silhouettes in Fig. 7B. Although at first glance, the shapes point to a frog-like amphibian, this now-informed audience can easily distinguish the silhouette of the toad from that of the frog. The conversation then steers into a discussion about the resistance of such species to changes in temperature, water availability, and natural rhythms. A study by a scientist working in the park has revealed that if current climate trends persist, 4 of the 17 common species of amphibians in the park are likely to survive, while 7 are likely to go extinct (Fig. 8A). A visitor is tempted to take comfort in the news that not all amphibians will vanish before another visitor regrets the loss of even a single species. The ranger seeds the ensuing discussion with the image in Fig. 8B—would we be willing to let go of a single species if it were the panda, the giraffe, the African elephant, or any of the iconic and much loved animals on the planet?

Discussion

iSWOOP serves as an on-the-ground studio and laboratory for designing and experimenting with such material and interpretive approaches. Because of the iSWOOP project, visual material like those described above are featured on a regular basis at five national parks in conversations capably facilitated by dozens of park rangers in contact with thousands of visitors. In the coming years, the iSWOOP team will continue to study the images, formats, presentation styles, and visitor interactions showcasing current scientific research.

Developing visual literacy is not a trivial undertaking. It will require deliberate and reiterative practice (Little et al. 2015). For many adults and youth, daily life is media-rich, yet requires savviness and opportunities to practice meaning-making and interpreting the output of created and consumed images, video, and other types of graphic representations. Programs like iSWOOP can offer a safe space for adults and youth to apply and refine a subset of their visual literacy skills, particularly those that require interpreting, analyzing, and evaluating visualizations. Image generation is a critical component. We anticipate exploring the potential for generating visualizations—air drawing stress levels, a stick-in-dirt sketch of a line showing predictions for JOTR survival, the visitors taking over a docent's tablet and shading to show relative importance of different factors, or taking their own shots with the infrared setting on their cell phone cameras to experience their surroundings through a different lens.

The design principles outlined here are suggestions for priorities and the language that allows partnerships among scientists, designers, and environmental educators to integrate existing material into narrative sequences. Values of flow, sequence, and continuity lend thematic coherence and stylistic organization, with compelling presentation. Leveraging functional minimalism, multimodality, novelty, and dynamism, the principles not only foreground an aesthetic and visual vocabulary, but take into account that for STEM learning to occur, the viewer has work to do. Viewers can make meaning, decode, and decipher with confidence in the presentation and the interpreter. A skilled ViA presenter directs attention to parts of the presentation best suited for the audience's cognitive involvement at each moment (Gibson 1969).

Some may take issue with the separation of design principles, the names assigned, or the exclusion of other design formulations. Nevertheless, these constructions are a serviceable starting point to determine the level of detail that will make an impact without bogging down the conversation or overloading the viewer with information to decode. Ultimately, the point is to communicate efficiently and to take advantage of the many affordances of visual imagery.

ViA treatments are parsimonious and purposeful in their design. We argue that such a communication approach is not only suitable for iSWOOP, but more generally for efforts in science communication. This approach can support interpreters' versatility in using imagery to support storytelling, as well as peer-to-peer exchanges as often are prompted among park visitors encountering such visual material.

Scientists and designers collaborating on visual material can use the ViA design principles and Visualization Spectrum as touchstones when considering pros and cons of design choices, balancing their overall development effort, accuracy, and richness of content representation with audience experience and benefit. Design and visualizations pose tremendous opportunities for public engagement with scientific ideas and phenomena. Design sensibility, in concert with the versatile representational vernacular of data visualizations, can form a basis for non-scientists' appreciation of scientific content.

Acknowledgments

We thank park interpretive and education resources and management staff from ACAD, CAVE, INDU, and JOTR National Parks, as well as NPS leadership and our advisory board members. We are also grateful to the Design Team at ASAP Media Services, University of Maine, the project illustrators and animators Dennis Nikolaidis, Chris Tullar, and Brittani George, and the generous and dedicated iSWOOP featured scientists Juniper Harrower, Bob Brodman, Jacquelyn Gill, George Jacobson, Steve Norton, Katie Percy, and Tatjana Hubel. Two anonymous reviewers significantly improved the quality of the manuscript. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the view of the National Science Foundation or the Society for Integrative and Comparative Biology.

Funding

The iSWOOP project was made possible with support from the National Science Foundation DRL-123030 and DRL-1514776. The symposium, Science in the Public Eye: Leveraging Partnerships, was made possible with support from the National Science Foundation DRL-123030 as a part of the iSWOOP (interpreters and Scientists Working On Our Parks) project. The following divisions of the Society for Integrative and Comparative Biology have generously supported the symposium: Division of Animal

Behavior, Division of Comparative Biomechanics, Division of Comparative Endocrinology, Division of Ecoimmunology and Disease Ecology, Division of Neurobiology, and Division of Vertebrate Morphology.

References

Adichie CN. 2009. The danger of a single story. TED Talk. (https://www.ted.com/talks/chimamanda_adichie_the_danger_of_a_single_story? referrer=playlist-the_most_popular_talks_of_all#t-39147).

Allen L, Char C, Hristov N, Wright T, Merson M. 2018. Beyond the brown bag: designing effective professional development for informal educators. Integr Comp Biol (doi: 10.1093/icb/icy026).

Bearne E, Wolstencroft H. 2007. Visual approaches to teaching writing multimodal literacy 5–11. London: Paul Chapman Publishing.

Bhojwani P, Lord B, Wilkes C. 2009. I know what to write now: engaging boys (and girls) through a multimodal approach. Leicester: UKLA.

Brodman R. 2009. A 14-year study of amphibian populations and metacommunities. Herpetol Conserv Biol 4:106–19.

Collins BL, Lerner ND. 1982. Assessment of fire-safety symbols. Hum Factors 24:75–84.

Dahlstrom MF. 2014. Using narratives and storytelling to communicate science with nonexpert audiences. Proc Natl Acad Sci U S A 111:13614–20.

Dondis DA. 1973. A primer of visual literacy. Cambridge (MA): MIT Press.

Doumont JI. 2002. The three laws of professional communication. IEEE Trans Prof Commun 45:291–6.

Doumont JI. 2005. The cognitive style of PowerPoint: slides are not all evil. Tech Commun 52:64–70.

Duarte N. 2008. Slide:ology: the art and science of creating great presentations. Sebastopol (CA): O'Reilly Media

Ells JG, Dewar RE. 1979. Rapid comprehension of verbal and symbolic traffic sign messages. Hum Factors 21:161–8.

Feynman Richard P. 1995. [1963]. Six easy pieces: the fundamentals of physics explained. Introduction by Paul Davies. London: Penguin Books. p. ix.

Gibson EJ. 1969. Principles of perceptual learning and development. New York (NY): Appleton-Century-Crofts.

Graesser AC, Ottati V. 1995. Why stories? Some evidence, questions, and challenges. In: Wyer RS, editor. Knowledge and memory: the real story. Hilldale (NJ): Lawrence Erlbaum. p. 121–32.

Green D. 2006. Historically underserved students: what we know, what we still need to know. New Dir for Community Coll 2006:21–8.

Gross AG, Harmon JE. 2009. The structure of PowerPoint presentations: the art of grasping things whole. IEEE Trans Prof Commun 52:121–37.

Gulino PJ. 2003. Screenwriting: the sequence approach. New York (NY): Continuum.

Ham S. 1992. Environmental interpretation: a practical guide for people with big ideas and small budgets. Golden (CO): Fulcrum Publishing.

Hattwig D, Bussert K, Medaille A, Burgess J. 2013. Visual literacy standards in higher education: new opportunities for libraries and student learning. Portal Libr Acad 13:61–89.

Jarman R, McClune B, Pyle E, Braband G. 2012. The critical reading of the images associated with science-related news reports: establishing a knowledge, skills, and attitudes framework. Int J Sci Educ B 2:103–29.

King LE. 1975. Recognition of symbols and word traffic signs. J Safety Res 7:80–4.

Laiser D. 2005. Drawing theories apart: the dispersion of Feynman diagrams in postwar physics. Chicago (IL): Chicago University Press. p. 4.

Lehto MR. 1992. Designing warning signs and warning labels: scientific basis for initial guidelines. Ergonomics 10:115–38.

Little D, Felten P, Berry C. 2015. Visual literacy across the disciplines: new directions for teaching and learning. San Fransisco: Jossey-Bass, Wiley.

MacArthur C. 2014. Changing lives, saving paper and engaging visitors: technology and the acadia experience. Final Report on Summer 2014 Research Studies (http://api.ning.com/files/kV4MbYiv7oT1o2MtPdOIBXZmHYj1xG8GySMTGBkAgPmuh3uWqAsB3oO5z-a76htUKN1urVBafeGck6LDHIiNTYCq0rY65vPe/FinalReport.pdf).

Magurno AB, Kohake JR, Wogalter MS, Wolff JS. 1994. Iterative test and development of pharmaceutical pictorials. Ergon Des 4:360–2.

Marino M, Koke J. (2003). Face to face: examining educational staff's impact on visitors. ASTC Dimensions (http://astc.org/pubs/dimensions/2003/jan-feb/index.htm).

McDougall SJP, Curry MB, de Bruijn O. 2001. The effects of visual information on users' mental models: an evaluation of pathfinder analysis as a measure of icon usability. Int J Cogn Ergon 5:59–84.

Merson M, Allen LC, Cox P, Hristov NI. 2016. Roving with a digital visual library: increased learning opportunities at Carlsbad Caverns National Park. J Interpret Res 21: 9–29.

Merson M, Char C, Hristov N, Allen L. 2017. Seeking park-based science information: interpreters at the gate. George Wright Forum 34:368–80.

Merson M, Allen LC, Hristov NI. 2018. Science in the public eye: leveraging partnerships—an introduction. Integr Comp Biol (doi: 10.1093/icb/icy034).

Metros SE. 2008. The educator's role in preparing visually literate learners. Theory Pract 47:102–9.

Nathanson S. 2006. Harnessing the power of story: using narrative reading and writing across content areas. Read Horiz 1:1–26.

Nemirovsky R, Noble T. 1997. On mathematical visualization and the place where we live. Educ Stud Math 33:99–131.

Norman DA. 1990. The design of everyday things. New York (NY): Doubleday.

Olson R. 2009. Don't be such a scientist: talking substance in an age of style. Washington (DC): Island Press.

Olson R. 2015. Houston, we have a narrative. Chicago (IL): The University of Chicago Press.

Paivio A. 1986. Mental representations. A dual coding approach. New York (NY): Oxford University Press; Clarendon Press.

Russell SJ, Corwin RB. 1989. Statistics: the shape of the data. Used numbers: real data in the classroom. Grades 4–6. Palo Alto (CA): Addison-Wesley Publishing Co.

Santa JL. 1977. Spatial transformation of words and pictures. J Exp Psychol Hum Learn Mem 3:418–27.

Schank RC, Abelson R. 1995. Knowledge and memory: the real story. In: Wyer RS, editor. Knowledge and memory: the real story. Hilldale (NJ): Lawrence Erlbaum. p. 1–86.

Serafini F. 2012. Expanding the four resources model: reading visual and multi-modal texts. Pedagog Int J 7:150–64.

Tufte ER. 1990. Envisioning information. Cheshire (CT): Graphics Press.

Tufte ER. 1997. Visual explanations. Cheshire (CT): Graphics Press.

Tufte ER. 2001. The visual display of quantitative information. Cheshire (CT): Graphics Press.

Tufte ER. 2003. The cognitive style of PowerPoint. Cheshire (CT): Graphics Press.

Tufte ER. 2006. Beautiful evidence. Cheshire (CT): Graphics Press.

Vezin JF. 1984. Apport informationnel des schémas dans l'apprentissage. Trav Hum 47:61–74.

Wong W. 1972. Principles of two-dimensional design. New York (NY): John Wiley & Sons.

Wong W. 1977. Principles of three-dimensional design. New York (NY): Van Nostrand Reinhold.

Wong W. 1993. Principles of form and design. New York (NY): John Wiley & Sons.

Zabrucky KM, Moore D. 1999. Influence of text genre on adults' monitoring of understanding and recall. Educ Gerontol 25:691–710.

Zimmer C. 2018. Science and scandal: reporting on science in an age of controversy, Plenary-1, Society for Integrative and Comparative Biology annual conference, 3–7 January 2018. San Francisco (CA).

Zimmerman HT, Land SM. 2014. Facilitating place-based learning in outdoor informal environments with mobile computers. TechTrends 58:77–83.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 127–139
doi:10.1093/icb/icy027
Society for Integrative and Comparative Biology

SYMPOSIUM

Cultivating Collaborations: Site Specific Design for Embodied Science Learning

Katherine Gill,* Jocelyn Glazier† and Betsy Towns1,‡,§

*PLA, Tributary Land Design, Durham, NC, 27707, USA; †School of Education, The University of North Carolina at Chapel Hill, Chapel Hill NC, 27599, USA; ‡Center for Design Innovation; §University of North Carolina School of the Arts, Winston-Salem, NC, 27127, USA

From the symposium "Science in the Public Eye: Leveraging Partnerships" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1] E-mail: townsb@uncsa.edu

Synopsis Immersion in well-designed outdoor environments can foster the habits of mind that enable critical and authentic scientific questions to take root in students' minds. Here we share two design cases in which careful, collaborative, and intentional design of outdoor learning environments for informal inquiry provide people of all ages with embodied opportunities to learn about the natural world, developing the capacity for understanding ecology and the ability to empathize, problem-solve, and reflect. Embodied learning, as facilitated by and in well-designed outdoor learning environments, leads students to develop new ways of seeing, new scientific questions, new ways to connect with ideas, with others, and new ways of thinking about the natural world. Using examples from our collaborative practises as experiential learning designers, we illustrate how creating the habits of mind critical to creating scientists, science-interested, and science-aware individuals benefits from providing students spaces to engage in embodied learning in nature. We show how public landscapes designed in creative partnerships between educators, scientists, designers, and the public have potential to amplify science learning for all.

Introduction: the (dis)embodied nature of teaching and learning

Historically, psychologists and other scientists have separated mind from body, to perceive them as peripherally connected but not integral to one another (Descartes 1952,1980; Russell 1990). Schools and universities generally privilege disembodied practises that maintain this mind/body dualism. In this dualistic approach, "[e]xcept as a container for the mind, [the body] has no significance" (Paechter 2006, 123). Recently, cognitive scientists have prompted reconsideration of the mind/body dualism, reminding us that thinking is shaped by and with our bodies and actions (Abrahamson and Lundgren 2014). The study of embodied cognition suggests, "Human cognition is deeply rooted in the body's interactions with its physical environment" (Lindgren and Johnson-Glenberg 2013, 446). Indeed, as Gibbs (2005) cautions, "We must not assume cognition to be purely internal, symbolic, computational, and disembodied, but seek out the gross and detailed ways in which language and thought are inextricably shaped by embodied action" (Gibbs 2005, i). While true across all disciplines, the role of the body in learning may be especially influential in the sciences (Alsop 2005; Liben et al. 2011; Bajak 2014; Kontra et al. 2015; Weisberg and Newcombe 2017). Indeed, "STEM education initiatives may particularly benefit from embodied cognitive practices because STEM disciplines rely on representation systems that require sensory encoding . . . and are nevertheless dependent on highly abstract, formalized symbol systems (e.g., those used in . . . chemistry). Students need a 'way in' to linking sensory representations with abstractions" (Weisberg and Newcombe 2017). That "way in" requires shifting not only how but also where we teach science.

Examples mount to suggest that "if cognition is embodied and if embodied learning is more efficient for cognitive development, then maybe schools

Advance Access publication May 21, 2018

should change their style of teaching to promote this kind of learning in students at all ages" (Ionescu and Glava 2015, 10). Though we increasingly see that hands-on, inquiry-driven learning effectively cultivates the critical and creative thinking skills needed for discovery and innovation (National Research Council 2000; Barron and Darling-Hammond 2008; Roberts 2015), mainstream schools and universities prove difficult ships to turn, freighted with policies that oblige teachers to focus on fact delivery and assessment. Traditional science labs seldom provide opportunities for open-ended, active, embodied learning. Instead, accountability measures and pressures of standardized assessment at all levels constrain teaching and learning, hampering imagination and curiosity that deepen into rigorous inquiry. Furthermore, "(e)mbracing the body as an active and meaningful part of the learning process is a . . . daunting ideological and pedagogical hurdle, given our habituated reluctance to consider cognition as embodied" (Blatt-Gross 2015, 138), adding challenges to implementation.

In the design cases described below, which bring together our professional experience in Landscape Architecture (Gill), Curriculum Design (Glazier and Towns), Education (Glazier), and Public Art (Towns), we illustrate the development of learning spaces that invite students to experience science in embodied ways. We build from our argument that creating the habits of curiosity, empathy, inquisitiveness, observation and reflection, habits critical to the development of scientists and science-aware individuals, depends on giving students experiences in the natural world (Schwartz and Martin 2004; Leong et al. 2014).

Interdisciplinary collaborations: designers are scientists, scientists are designers

Since big freighters—traditional education spaces and methods—prove slow to change despite the demonstrated effectiveness of embodied learning (Singer et al. 2012; Freeman et al. 2014; Kontra et al. 2015), we, as designers, scholars, and educators have boarded exploratory vessels—alternative places of learning like farms, zoos, and museums. In our experience, these sites provide ideal grounds for prototyping alternatives. The challenge of wide-ranging audience expectations and typically small number of staff demand close collaborations to enable the success: staff from disciplines like art, design, science, and education work closely together in these alternative learning sites, bringing with them multi-disciplinary understandings. Referring to science museums, Sue Allen, Learning Research Director at the Exploratorium, writes: "We expect these institutions to provide a hugely diverse visiting public with entertainment, the freedom to choose their own path, follow their personal interests, do their own inquiry, and create their own meanings. Yet at the same time, we want our museums to be respected educational institutions where people can spend an hour and come away having learned some canonical science" (Allen 2004, S18). These seemingly conflicting demands of alternative learning sites depend on sustained interdisciplinary design collaboration.

In our work in and outside the school system, we have found the benefits of carefully designing and building interdisciplinary teams to shape embodied learning outcomes outweigh the challenges. In the design cases below, we show how, when interdisciplinary design teams are established at the outset of the planning process, and come together regularly to define, design, test, evaluate, and revise the design, the process results in flexible, innovative, and effective learning platforms (Fig. 1). The literature suggests—and our experience concurs—that true collaboration exists when partners come to the table early, on equal footing, and with equal interest in the questions and outcomes at hand (Drayton and Falk 2006; Munson et al. 2013). Moreover, in our work with scientists, we have found a necessary symbiosis: as Galatowitsch (1998) explains, "Science and design are complementary ways to generate knowledge (and therefore both are creative endeavors). Scientists solve problems inductively, forming generalized principles from specific observations. Designers use general principles to solve specific problems deductively" (102).

In our experience, the most effective collaborations between designers and scientists include participants from both disciplines who demonstrate capacity to practise deductive and inductive thinking. In essence, both think as scientists and both think as designers in and through this process of creating authentic learning applications. Collaborative, interdisciplinary teams built early, with attention paid to the design practise of establishing empathy for the team and needs of the project lead to powerful design outcomes. These outcomes benefit students (who experience more effective and engaging learning), scientists (who gain tools for communication, and an expanded pipeline of scientists and science interested), and designers (who attain an expanded field for impactful design practise) (Galatowitsch 1998; Munson et al. 2013).

Shifting learning landscapes

Because lived experience influences cognition, the environment where students learn impacts what

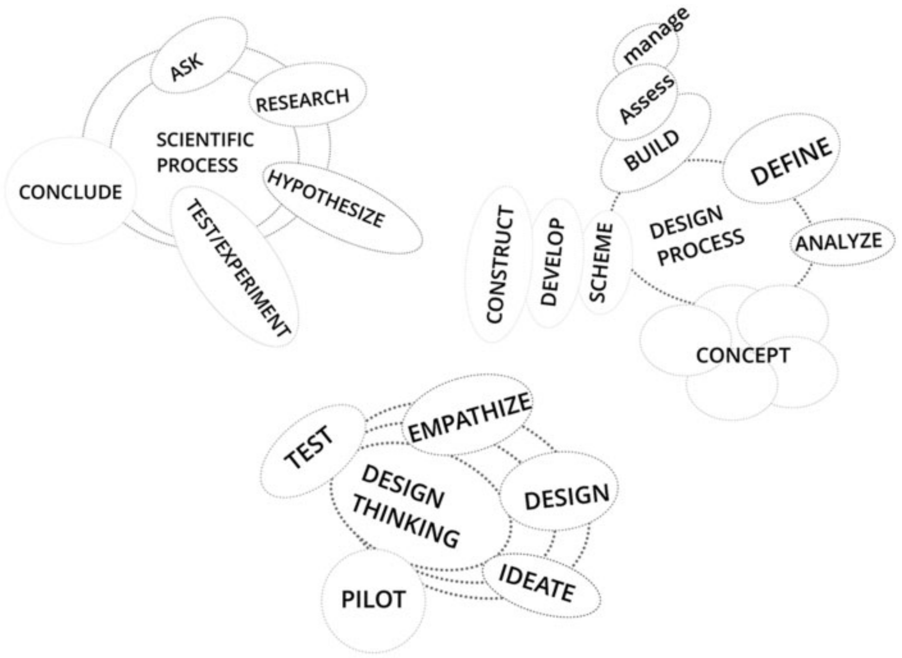


Fig. 1 The overlap of design thinking, design process, and scientific process: our methodologies for discovery and solution building are similar across disciplines. The typical design process starts with defining a design need, then goes through an analysis, then into concept building, program development, and then schematic, design development, and construction drawings. From this point, the design is built, and the programming and site are managed over time.

learning happens. Full-body experiences, which blend play and experimentation, can help students perceive science more positively. We argue that: "learning environments for math and science can be made more effective if they are designed to tap into bodily know-how that originates both from existing life experience and new learning experiences" (Abrahamson and Lundgren 2014, 11). Furthermore, the field of "embodied cognition has emphasized the role that the body and environment play in cognitive processing" (Weisberg and Newcombe 2017). School and university settings have looked similar for centuries; interdisciplinary collaborations between researchers, scientists, educators, and designers provide compelling opportunities to test new kinds of learning spaces that put embodied learning into practise.

Carefully designed, spaces of informal learning build young people's sense of efficacy, curiosity, and capacity for learning (Allen 2004). Because traditional labs and classrooms seldom have institutional flexibility and space to facilitate these experiences, alternative learning habitats offer needed platforms. Our collaborative work helps us consider: What if we design experiential spaces where body and mind were encouraged to interact? Such habitats for learning and the experiences they can provide are important learning landscapes, particularly for sciences. Actualizing these designs depends on cultivating and managing public and private partnerships. Bringing diverse, interdisciplinary voices—from funders to educators to scientists to designers—together to create and use spaces of natural learning introduces greater opportunity for innovation across disciplines.

Two collaborative design processes we have led—the North Carolina Zoological Park (NC Zoo) *Treehouse* Master Plan and the Durham Public Schools Hub Farm (DPS Hub)—demonstrate the development and use of habitats for fostering inquisitive minds of future scientists and offer insight as to how we can facilitate interdisciplinary collaborations. These sites provide interdisciplinary teams space to prototype immersive learning experiences, and platforms to conduct research on science learning and design effectiveness. We illustrate our reliance on design practise to create habitats and experiences that can build visitors' capacity as independent learners. The design cases illustrate: our process, fruitful and frustrating collaborations and partnerships, and promising practises for authentic science learning and assessment. The design cases further demonstrate that, thoughtfully led, the design process can build the collaborative team even as it builds the design.

DESIGN CASE 1: *Adversaries to Team—The NC Zoological Park Treehouse Master Plan*

The North Carolina Zoo (NC Zoo) is a natural habitat zoo that prioritizes the health and well-being of the animals and plants, emphasizing the environmental and educational goals of conservation of species and habitat. This means site-lines are carefully constructed so animals on exhibit seldom see visitors, and have huge spaces to roam. Therefore, visitors may find that, seen from hundreds of yards away in their expansive, natural-appearing enclosures, water buffalo and elephants resemble ants and beetles. At the natural habitat zoo, visitors do not feed, touch, or otherwise play with zoo animals. Insofar as possible, lived experience of the animals mimics their experience in the wild.

The design question

The team from SolidZebra, led by Betsy Towns as artist and site designer and Katherine Gill as co-site designer and landscape architect, was challenged with how to create embodied biology learning experiences when visitors and animals are separated from one another. Our scope of work called for master planning an exhibit directed at children. At the surface, it appeared to the NC Zoo staff that the principled, conservationist design of exhibits in the zoo opposed the zoo educators' goals of teaching scientific and ecological mindset through close engagement with living exhibits. The research and discovery phase of the design process—involving collaboration between our team of designers and artists, and NC Zoo exhibit designers, scientists, and educators—demonstrated that embodied learning experiences exceed pedagogical outcomes for all visitors compared to content-based interpretives. First, zoo educators, and, somewhat more slowly, zoo horticulturalists, biologists, and veterinarians, came to see that designing embodied learning experiences could substantially impact the environmental, cognitive, and pedagogical outcomes for visitors of all ages, and that we could identify ways to achieve these without impacting zoo exhibit species (Allen 2004; Leong 2014). By engaging all parties equally in the design process from start to finish in periodic full-day design charrettes, we became a cohesive team. The method led to an authentically shared understanding of the value of embodied practise to prepare learners to become inquisitive, empathetic inhabitants of the natural world, and to engage with science material more substantively. "As designers engage in a process of developing an image, representing it, and then testing their ideas, they ... provide a catalyst for change, for achieving an outcome, and, most important, for facilitating a thinking process. In a thoughtful process, the designer takes into account what exists and provides an opportunity for the players to express themselves, to be effective, and to feel empowered. The designer's role is a critical part of the triangle of players who together create a place that goes beyond the narrow and timid to encompass the 'enchantments of childhood'" (Stine 1997, 7). With a team more open to the high-impact practises of embodied learning, the informal spaces of the zoo offered an ideal location to prototype and test learning results more effectively than within traditional schools (e.g., Barron and Darling-Hammond 2008; Roberts 2015). The design process allowed us to turn opponents into collaborators and discover opportunities to create learning experiences that propel the goals of all.

Design strategy emerges

Based on the areas of agreement discovered in stakeholder workshops, the design team (Towns and Gill) made two decisions that shaped the design of the Master Plan: rather than designing animal encounters involving the zoo wildlife collection, the exhibit would create spaces apart from the zoo animal habitats for "parallel encounters" with familiar species that visitors could transfer to their observation and reflection on the zoo animal exhibits. Animal encounters in the design focused on pet species (dogs, rabbits), indigenous species abundant on the property (squirrels, ants, owls, black snakes), and species with history of domesticity (goats). The choices avoided bringing visitors into contact with exotic collections, while engaging the expertise of zoologists, conservationists, and horticulturalists in creating relevant parallel experiences; together we considered how scientific content could become 'hands-on' engagement.

Defining the exhibit

At this point, we proposed that the NC Zoo Master Plan focus on three strategies to achieve the conservation education mission: (1) Creating play opportunities that duplicate and repeat behaviors that visitors watch animals do in their own habitats (empathy building); (2) Designing spaces for imaginative independent play (creativity and curiosity); and (3) Establishing pivot points between the visitors' inner and outer selves, giving them opportunities to reflect on physical engagements to take with them the traditional 'look but don't touch' exhibits of the rest of the zoo.

Following Discovery phase, the exhibit emerged around these strategies. A preliminary concept, *The Treehouse*, created immersions in each strategic practise. For example, to build empathy through parallel experiences, we created sequences of exhibits around climbing, home building, and food-gathering. The dramatic centerpiece is a large treehouse in the deciduous forest (Fig. 2). Each iteration of the design process brought scientists, educators, and designers together to critique and evaluate the accuracy and effectiveness of the ways that designers had put visitors into motion in relation to zoo ecology. Optimally, zoo visitors would emerge from the experience with an increased alertness to qualities of locomotion (especially adaptations that enable mammal survival in treetop habitat), with a sense of species interactions (squirrels and oak interdependence), and practise/warm-up in observing wildlife (embodying squirrel feeding, climbing, and nesting behaviors), all concepts with transferability to exhibits throughout the zoo (Fig. 3).

Implications

The Master Plan relies on meaningful engagement with plant and animal species tolerant of human interactions to create openness to learning about animals and plants in the zoo exhibits. Experiences that engage biomechanics, movement, interaction, manipulation, and many senses and modes of cognition offer potential to reach many different developmental levels and learning styles and capacities. In parallel, repeating play experiences creates capacities necessary for observing and reading that take prominence at zoo-interpretive exhibits (Fig. 4). When designs like this work effectively, we see an elevation of the kinds of questions visitors take time to develop (Bell et al. 2009). At the traditional zoo with caged animals, children might ask their parents: "Why is the lemur looping the same path again and again?" as the children experiment with their own loops on trails. At the natural habitat zoo, they might wonder: "Why can't I see the lemur?" At the natural play enhanced zoo, children might consider, as they climb structures and observe animals climb: "Why do lemurs have long front legs? Why do goats have four legs that are the same? and why do we climb on two legs?" It's not unusual for visitors to try out or mimic other ways of climbing to mimic those of the animals they see (Falk et al. 2008).

Commentary

In the NC Zoo Master Plan process, bringing the diverse perspectives of designers, scientists, and educators together made it possible to design playful, open-ended, embodied engagement that led to question-finding and problem solving, which build science-learning skills (Ellsworth 2004). Designing for open-ended and learner-driven play requires the institution and the educator to release some degree of control over specific content delivered. The designer forfeits some control in collaboration with the users: "Designing for open-ended play means taking a risk . . . . As a designer you do not know at the start of the project what the outcome will be. You have some assumptions, but these assumptions can turn out to be wrong" (de Valk et al. 2013, 98). Thus, the process corresponds with the experiences we shape for learners—it takes as its starting point open-ended play, examines judgments and embraces risk, experiment, and prototyping as strategies to reveal and exceed assumptions and limitations, and creates a climate for reflection, critique, and adaptation. Designing spaces for "knowledge in the making" (Ellsworth 2004) requires a process of "design in the making" and has given us routes to new ways of thinking about design, teaching, and learning. Working with designers can introduce scholars in all fields to new tools, methods, and places of learning that can increase the reach and impact of their pedagogy and research. The collaborative Master Plan design process at the NC Zoo, which involved staff Scientists, Educators, and Curators and Gill and Towns as Facilitators and Designers, led the Zoo to consider new strategies for embodied learning throughout their exhibit design.

Fig. 2 Illustration by the designers showing the main treehouse: webs, log-balance, and tunnel scramble draw young people into the canopy and challenge them to move through space in ways that engage their whole bodies in the treetops in the kinds of movements they see squirrels achieve in the adjacent trees. These climbing experiences lead visitors to nest building materials like those squirrels employ in the highest level of the trees, and to acorn gathering and stashing points throughout the entire treehouse exhibit. Feeders encourage the native squirrels to platforms in the canopy, and viewing stations give visitors practise at the kind of observation "work" they will do with the zoo exhibit animals throughout the park.

Fig. 3 The designers' sketches show climbing-experiences throughout the exhibit that parallel behaviors of the animals located there. A goat treehouse designed with rustic materials and same saturated color points as the children's treehouse lets visitors see how kid goats and kid humans climb in similar and different ways; dog and squirrel obstacle courses build on this integrative thinking through engaging repetition; oversized blades of grass and replicas of native ants invite visitors to climb in and explore.

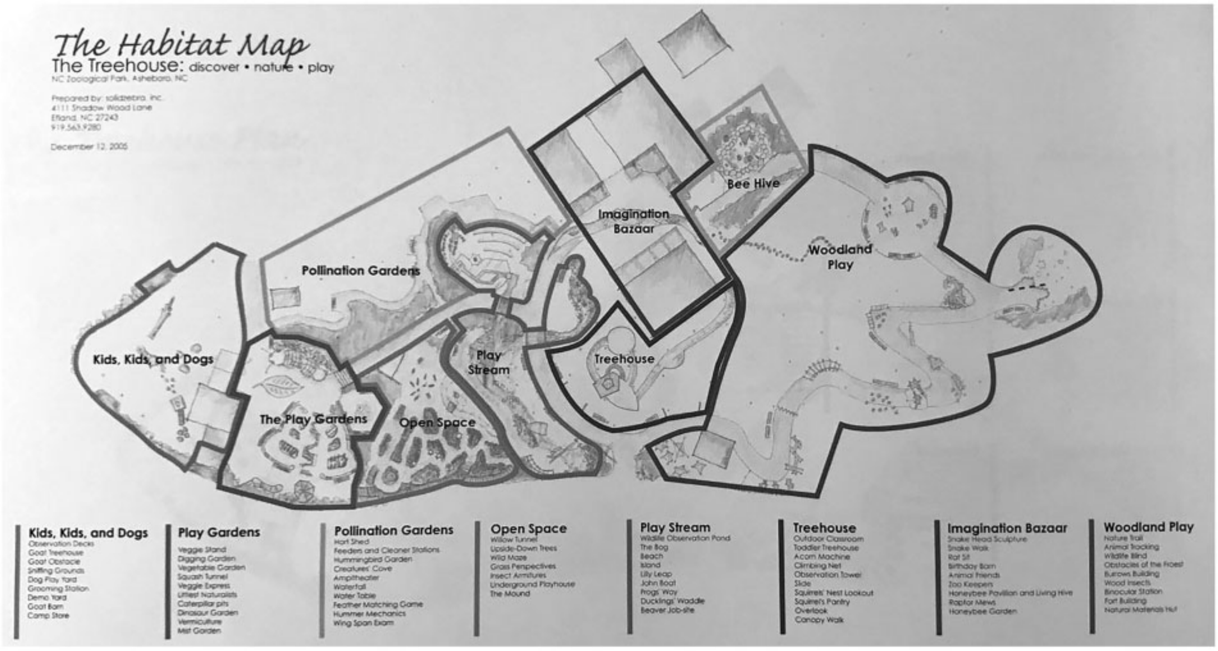


Fig. 4 The designers' diagram illustrates various habitats represented in the Master Plan.

DESIGN CASE 2: *Cultivating Embodied Learning by Engaging Community Partners, Scientists, Administration, Teachers, Volunteers, and Students in adapting Fallow Lands into Environments where Students Delight in Learning Outdoors.*

The Durham Public Schools Hub farm is a 32-acre outdoor learning lab initiated in 2011 by a small group of stakeholders interested in creating opportunities for all 32,000 district students to engage in outdoor, project-based health, and science learning. As landscape architect and founding project developer, Katherine Gill helped develop creative strategies for collaborations and to facilitate a strategic plan and design for how the school system could put this fallow site to work for experiential learning. The engaged team that led the initiative included a committed member of the district's Board of Education; the district Director of Career and Technical Education, and leaders and scientists from educational non-profits in the community. A driving design question was: How might the design of the Hub Farm complement and extend science learning that happens inside school walls? (Fig. 5)

From a design perspective, the Hub Farm differs from typical landscape architecture projects where designers are hired to create a design from concept to construction, and complete the project before it is used. The Hub Farm is unique: it is an environment where design emerges as students and teachers engage in this space and where outcomes evolve based on visitors' own questions, lives, and experiences on the site. The design concept for the Hub Farm is to provide an open-ended experience for all types of learners, providing a framework and the structure for the exploration of multiple learning outcomes.

With very little money, a completely overgrown site, and limited leadership from the highest levels of the administration, it was critical to begin the design process by focusing on the strengths inherent in the site and the people who would use it. In other words, the collaborations became the project, and the activation of those partnerships became critical to the Hub Farm growing into a vibrant learning lab. At the beginning of the design process at the Hub, we identified the type of collaborations and partners in the community with expertise in providing programming and curriculum for students but that were limited in their ability to reach students within the school system. The Hub Farm site is comprised of a diversity of Piedmont forest types and unusual volcanic granite rock formations. The hydrology includes stormwater from neighboring roads, parking lots, and rooflines that flow into a perennial stream, wetlands, and two agricultural ponds. Given these site features, we were immediately able to inhabit, experience, and bring to life the natural history of NC geology, ecology, climate change, and land use history through partnerships with organizations in the area that are doing related research and seek to provide outreach assistance to the community: NC State University's Soil Sciences Department; UNC College of Education, Durham County Soil and Water Conservation, NC State Agricultural Extension Water Quality experts, and many others (Fig. 6).

The Hub Farm acts as the lab to pilot and assess embodied teaching and learning outcomes from which further programming across the district and state can develop. It is the hub from which spokes emerge, reaching across schools and organizations (Fig. 7). For example, through a collaboration with the Durham County Public Health Department, the Hub Farm implemented an innovative teaching approach which we named *Seed to Belly.* The collaboration between the Hub Farm, the schools, and the Health Department nutritionists enabled children to experience full cycles of the food system and nutrition processes firsthand (Fig. 8). Providing embodied learning opportunities for K-12 students at the hub farm is paramount. However, what happens when students step back into traditional school contexts? How can embodied science learning in this context stretch back to schools? To that end, we partnered with Jocelyn Glazier, faculty in the School of Education at the University of North Carolina, who works with K-12 teachers across multiple disciplines. Recognizing the impact of experiential learning on students, Jocelyn wondered how to better support teacher training in this pedagogy. How, for example, would science teachers teach authentically if they themselves experienced only disembodied science learning?

Design strategy

An ongoing summer partnership with the UNC Masters in Education (MEDX) program and the Hub Farm works to support experiential teacher learning about science through implementation of the design process. The design process during these summers consists of: (1) Framing a project for teachers and students to implement that would integrate science learning in the design-build process; (2) Introducing the general steps within the design process; (3) Reminding teachers and students to expect the ambiguity of many possible solutions, and that working through this ambiguity was part of the design challenge. Engaging in the process provides the next set of questions, answers, and challenges.

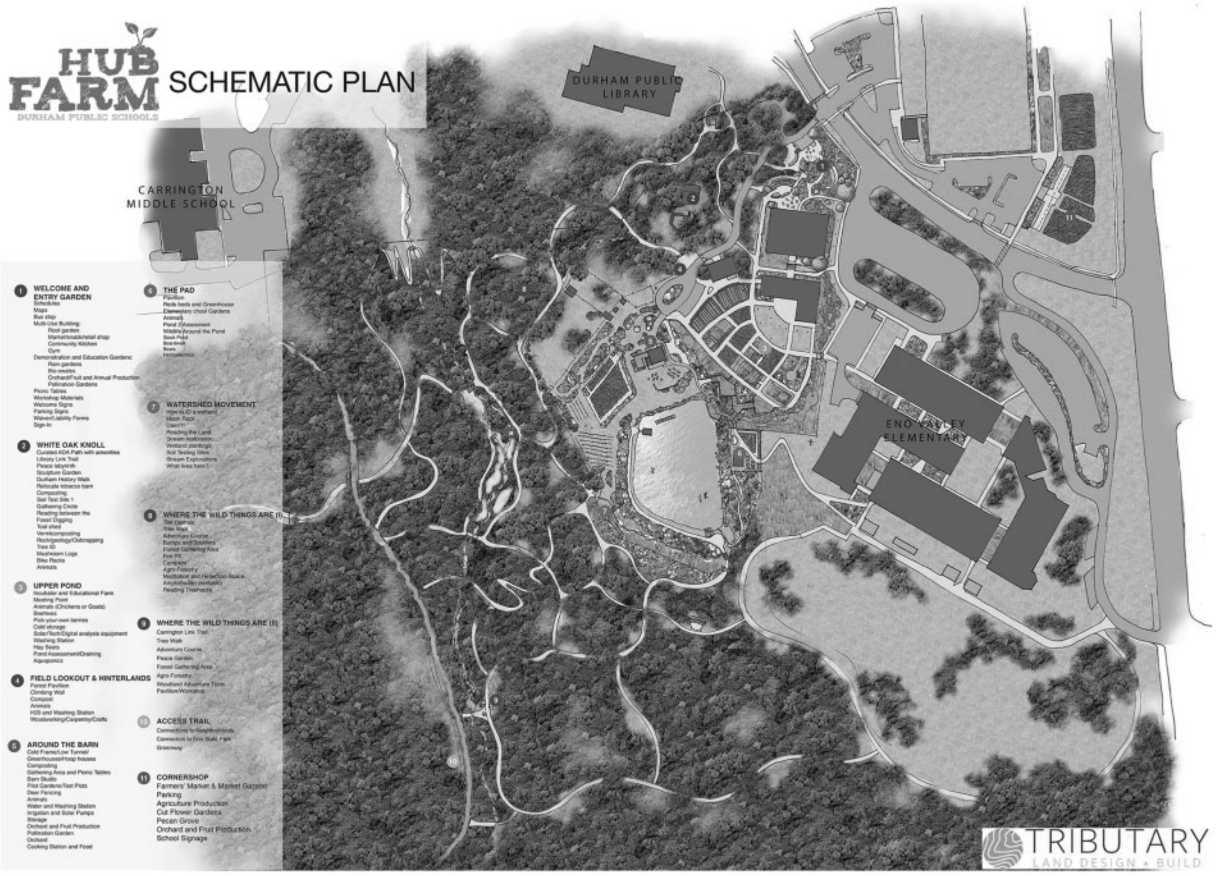


Fig. 5 The Hub Farm Master Plan plays off the natural habitats of the site to afford various exploration and science-based learning opportunities. The Master Plan also references the types of partnerships, collaborations, and student-run citizen-science initiatives that may be incorporated into the overall program.

Teachers and students familiar with the scientific process found key correlations with the design process.

Over the last 5 years, depending on the environmental, practical, and curricular needs of the space, MEDX teachers have created curriculum kits on water quality of ponds on site; built learning spaces along a path that connects the public library next door to the Hub Farm; and built gates and bridges that protect animals, and subtly invite or dissuade students from entering the farm. Each of these examples of spaces built by teachers offers poignant snapshots of embodied learning: a teacher knee deep in water who discovers how to measure the angle needed to support an 8′ wide bridge; the teachers' sense of accomplishment and satisfaction at seeing the gate they built from downed limbs; the shared smile of teacher and student discovering not one but seven different invertebrates in the bucket of water they pulled out of the pond together (Fig. 9). These outcomes were anticipated and surprising all at once. They were framed for the teachers with enough ambiguity to enable them to engage in necessary risk taking, initiative, and play. By following the design process, the teachers could engage in rigorous, hands-on learning while changing the landscape to support the learning of the next visitors to the Hub. Too often, teachers and students alike are invited into outdoor learning spaces that are closed-ended, exhibits that tell rather than show, that are hands-off rather than hands-on, that establish set questions and answers rather than opportunities to explore. When outdoor spaces are designed to enable authentic engagement with materials and opportunities to literally and figuratively fall into learning, scientific inquiry can blossom. The boundaries of spaces like the Hub Farm stretch to meet the questions and curiosities of those who visit.

Commentary

The Hub Farm enables open-ended opportunities for learning with varied outcomes that pivot the learner in new directions. The purposeful design concept of the farm leads to multiple experiences that lead in

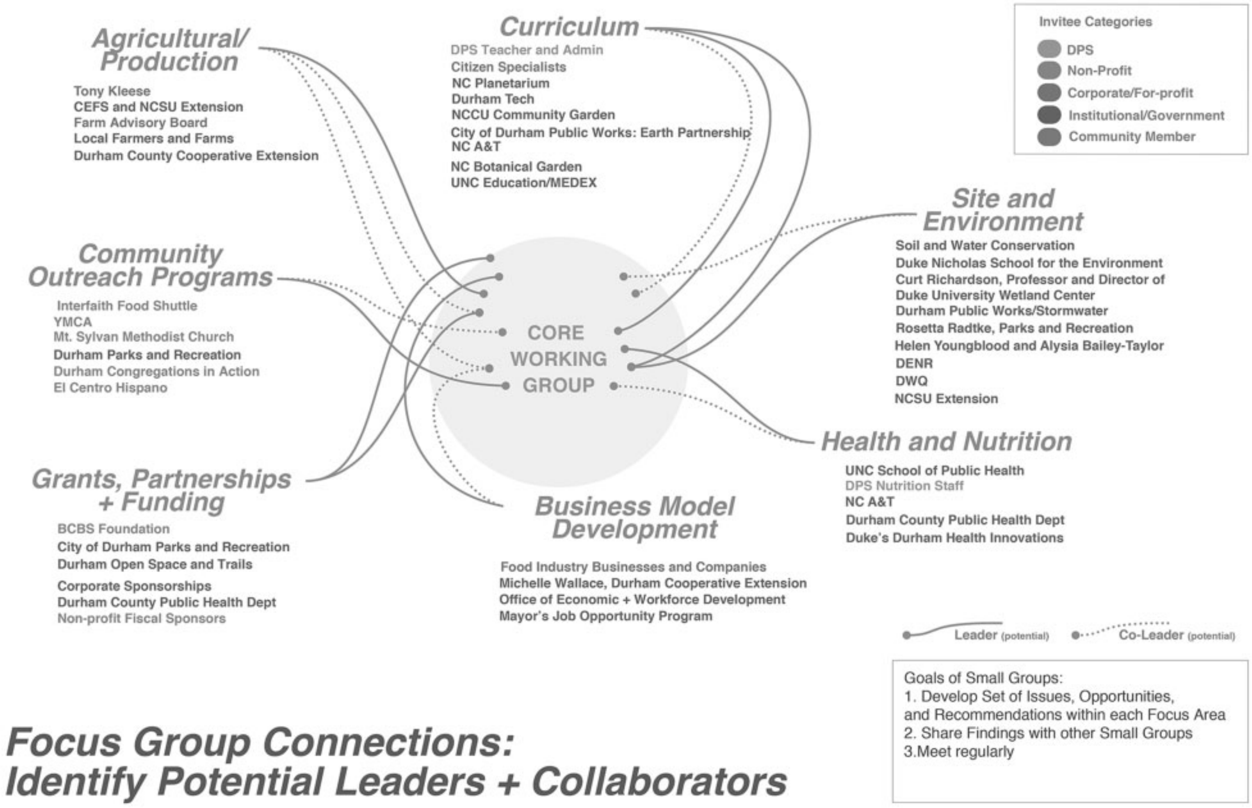


Fig. 6 A diagram of the potential partnership relationships across key programming goals and site features.

turn to a series of next challenges. Each season brings a new and different problem that demands authentic problem solving. The farm strips away the traditional boundaries of teaching and learning behind the walls of a classroom opening up new challenges for how to integrate learning at the Hub Farm with the learning that happens in the classroom. For teachers, the farm provides the critical space for teacher growth. Teacher trainings taught by scientists and professional experts in fields of science that not only bring scientific research into the hands of teachers but also tie-in the required learning materials of the classroom become very powerful tools that would lead to better integration from the Hub Farm back to the classroom. Teachers' experience of embodied learning allows them to imagine new possibilities for their classrooms. They are in turn able to create and develop inquiry-based and embodied experiences for their students. This experience cultivates autonomy, giving both teachers and learners a sense of authority, efficacy, and the opportunity to solve problems rather than having the right answers in mind. In essence, the teachers become scientists so that they can lead their K-12 students in becoming the same.

Discussion

As described, learning is as much physical as mental. "Embodied exploration and learning are inextricably intertwined" (Hirsch-Pasek and Golinkoff 2008). The habitats we present here reflect experiential spaces in which mind and body are invited to interact, providing important learning landscapes, particularly for science learning. As illustrated, these habitats provide opportunities for learning that is exploratory and open-ended. In order to build the desire and capacity for learning about science, we have to offer visitors experiences in well-constructed spaces like those above, that demonstrate to them pleasure, freedom, and autonomy to build their comfort in engaging in learning. Similarly, for learners of all ages to understand the relevance of the questions they consider in these spaces, they need exposure, guidance, and shared experiences with scientists, who, though they may be asking questions of a much higher level, are nonetheless, inquiring and learning in very similar ways to younger students. Scientists, who are willing to come to the table to work with designers and educators, can show us all the motivating environments that drive them into scientific inquiry.

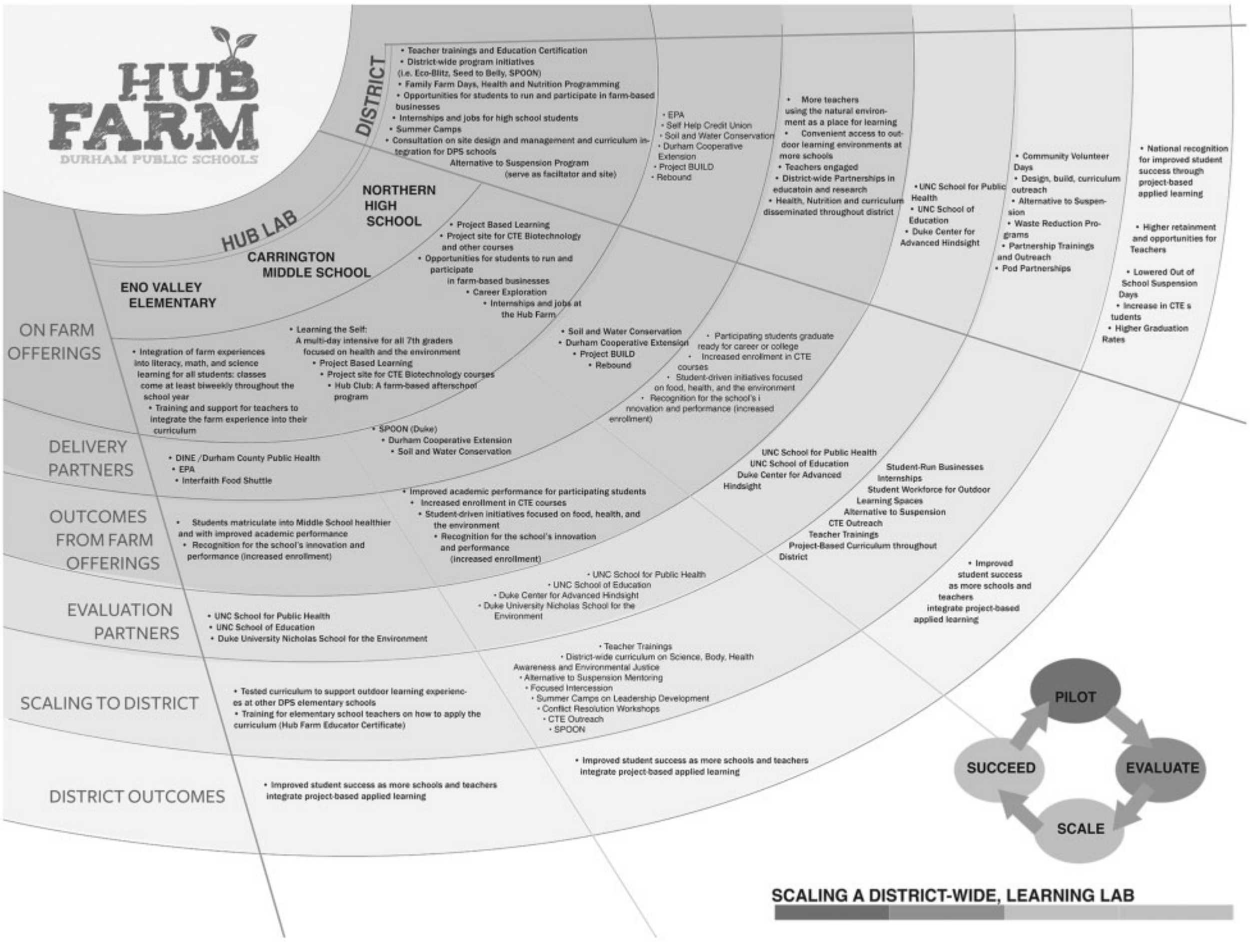


Fig. 7 Diagram showing scalable objectives tied to institutional partnerships with higher education.

Fig. 8 Food production becomes an embodied experience for students as they learn first-hand the role of soil, sun, water, and the ecological processes embedded in the food system while also learning to plant, harvest, prepare, and eat a fresh salad.

Fig. 9 UNC Masters in Education teachers busy in their new environment. It is hard to tell students from teachers in this embodied learning scene!

Conclusion and future directions

The careful design of outdoor learning environments, whether on farms, school grounds, museums, or zoos, plays a critical role in affording habits of mind that allow critical science thinking and learning to take root in students of all ages. These intentionally open-ended designs provide entry into authentic means of exploration, removing constraints of traditional school contexts. These sites also provide the learner the tools to discover interest and complexity and to locate the questions that plant the seeds for becoming scientists, artists, innovators, and educators. Effective design and partnerships play a critical role in taking this to capacity and applying it, making it useful, effective, and real. It also tasks designers to “do” design that meets educational and ecological imperatives and demonstrates models for collaboration and partnering with broad entities.

Our projects, involving design, implementation, and programming, have led us to the phase of careful assessment of the effectiveness of our work. What are indications of learning efficacy in these contexts? How do we know what science, what discoveries, visitors make in these landscapes? In these spaces, we seek to “measure” outcomes in ways that move beyond the traditional test. For example, we can observe students’ engagement with materials over time. As we observe students “muck around” in one of the ponds on the Hub Farm site, we can attend to how they engage with the water, with the mud, with one another. What sort of sense making are they engaging in? How are they talking about what they observe? How do they collaborate with one another? The freedom from traditional assessments and evaluation enables visitors to take risks with the materials, to play with outcomes that may seem implausible on the surface. In these spaces, they can make discoveries that venture beyond those we ourselves can imagine. The outcomes are not necessarily pre-determined. Indeed, here’s where scientific discoveries can happen.

Future assessment models may be qualitative and quantitative and can assess both process, outcome, conceptual understanding, and can drive the next set of questions to be explored. Visual mapping, behavior mapping, and conversation mapping (Beeken and Janzen 1978; Marcus 1990; Malone and Tranter 2003; Moore and Cosco 2010) can provide qualitative insight into spatial, temporal, and communication outcomes. With behavior mapping, we can gather data on how long someone spends within a particular exploration mode, in what areas, and with what diversity of spatial materials with which they are engaging. Conversation mapping can track the types of questions that are asked and gauge the complexity and relative interest in the subject, not to mention visitors’ understanding of the phenomenon being examined. Such evaluations can show how well students are working together and collaborating to solve a problem. Such mapping may also reveal how well diverse groups come together across gender, race, and age, by mapping the physical patterns in learning based on where students choose to be or who they choose to be with. Then evaluations can be made about the type of thinking and learning that occurs in each space.

Interdisciplinary collaboration in the design and assessment of outdoor learning landscapes enables us to offer students of all ages rich, complex, and educative possibilities. Places of outdoor learning offer critical opportunities to build understanding at multiple levels: visitors of all ages can find new ways to engage with the natural world, leading to increased comfort and enjoyment or emerging inquisitiveness and substantive new learning; designers gain opportunities to shape spaces that will be animated by the engagement of diverse leaders and learners, resulting in a continually evolving creative learning space; educators immersed in new ways of learning in landscapes like the NC Zoo and the Hub Farm can take this same learning to their own K-12 students; research scientists experience a place to examine their own questions of science in collaboration with citizen scientists and opportunities to test their powers of communication and contribute to a more educated populace.

Acknowledgments

We thank the extensive collaborative effort that went into the content of the design cases featured here: SolidZebra founding partner Mark Robinson contributed vision and expertise, architects David Ackerman and Anna Towns served as willing advisors. Curators at the North Carolina Zoological Park dedicated time and vision from start to finish to the Master Plan for the Children's Learning Center. For the Durham County Public Schools Hub Farm design case, we thank committed collaborators referenced in Figs. 6 and 7, especially DPS administration, staff, and students, particularly the farmer educator staff and the Director of Career and Technical Education, and students in the Masters for Experienced Teachers program in the School of Education at UNC who play key roles. We thank ICB editors, anonymous reviewers, and participants in the symposium for thoughtful contributions. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the view of the National Science Foundation or the Society for Integrative and Comparative Biology.

Funding

We thank organizers of the symposium, Science in the Public Eye: Leveraging Partnerships, made possible with support from the National Science Foundation DRL-123030 as a part of the iSWOOP (interpreters and Scientists Working on Our Parks) project. The following divisions of the Society for Integrative and Comparative Biology generously supported the symposium: Division of Animal Behavior, Division of Comparative Biomechanics, Division of Comparative Endocrinology, Division of Ecoimmunology and Disease Ecology, DNB (Division of Neurobiology) and Division of Vertebrate Morphology. Thanks to the Center for Design Innovation of UNC for funding travel to the conference, and for creating a climate for collaboration.

References

Allen S. 2004. Designs for learning: studying science museum exhibits that do more than entertain. Sci Educ 88:S17–33.

Alsop S. 2005. Beyond Cartesian dualism: encountering affect in the teaching and learning of science. The Netherlands, Dordrecht: Kluwer Academic.

Abrahamson D, Lundgren R. 2014. Embodiment and embodied design. In: Sawyer RK, editor. The Cambridge handbook of the learning sciences. 2nd ed. Cambridge (UK): Cambridge University Press. p. 358–76.

Bajak A. 2014. Lectures aren't just boring, they're Ineffective, too, study finds. Science (http://www.sciencemag.org/news/2014/05/lectures-arent-just-boring-theyre-ineffective-too-study-finds).

Barron B, Darling-Hammond L. 2008. Teaching for meaningful learning: a review of research on inquiry-based and cooperative learning. Powerful Learning: what we know about teaching for understanding. San Francisco (CA): Jossey-Bass.

Beeken D, Janzen H. 1978. Behavioral mapping of student activity in open-area and traditional schools. Am Educ Res J 15: 507–17.

Bell P, Lewenstein B, Shouse, A, Feder A., editors. 2009. Learning science in informal environments: people, places, and pursuits. Washington (DC): National Academies Press.

Blatt-Gross C. 2015. Review of moving ideas: multimodality and embodied learning in communities and schools. JoLLE 11:138.

de Valk L, Bekker T, Eggen B. 2013. Leaving room for improvisation: towards a design approach for open-ended play. In 12th International Conference on Interaction Design and Children, New York. p. 92–101.

Descartes R. 1980. Discourse on method and meditations on first philosophy, DA Cress, trans. Indianapolis (IN): Hackett Publishing Co.

Descartes R. 1952. Descartes' philosophical writings, selected and translated by NK Smith. London: Macmillan.

Drayton B, Falk J. 2006. Dimensions that shape teacher–scientist collaboration for teacher enhancement. Sci Educ 90:734–61.

Ellsworth E. 2004. Places of learning: media, architecture, pedagogy. New York (NY): Routledge.

Falk JH, Randol S, Dierking LD. 2008. The Informal Science Education Landscape: A Preliminary Investigation. Washington (DC): Center for Advancement of Informal Science Education.

Freeman S, Eddy SL, McDonough M, Smith MK, Okoroafor N, Jordt H, Wenderoth MP. 2014. Active learning increases student performance in science, engineering, and mathematics. Proc Natl Acad Sci U S A 111:8410–15.

Galatowitsch S. 1998. Ecological design for environmental problem solving. Landscape J 17:99–107.

Gibbs R. 2005. Embodiment and cognitive science. UK: Cambridge University Press.

Hirsh-Pasek K, Golinkoff RM. 2008. Why Play = Learning. In: Tremblay RE, Barr RG, Peters RDeV, Boivin M, editors. Encyclopedia on Early Childhood Development [online]. Montreal, Quebec: Centre of Excellence for Early Childhood Development. p. 1–7.

Ionescu T, Glava A. 2015. Embodied learning: connecting psychology, education, and the world. Studia Ubb Psychol - Paed LX: 5–17.

Kontra C, Lyons D, Fischer S, Beilock S. 2015. Physical experience enhances science learning. Psychol Sci (doi:10.1177/0956797615569355).

Leong LYC, Fischer R, McClure J. 2014. Are nature lovers more innovative? The relationship between connectedness with nature and cognitive styles. J Environ Psychol 40:57–63.

Liben L, Kastens KA, Christensen AE. 2011. Spatial foundations of science education: the illustrative case of instruction on introductory geological concepts. Cogn Instr 29:45–87.

Lindgren R, Johnson-Glenberg M. 2013. Emboldened by embodiment: six precepts for research on embodied learning and mixed reality. Educ Res 42:445.

Malone K, Tranter P. 2003. Children's environmental learning and the use, design and management of school grounds. Child Youth Environ 13 (http://www.colorado.edu/journals/cye/13_2/Malone_Tranter/ChildrensEnvLearning.htm, accessed February 12, 2013).

Marcus CC. 1990. From the pragmatic to the spiritual. In: Altman I, Christensen K, editors. Environment and behavior studies: emergence of intellectual traditions. New York: Plenum Press. p. 111–40.

Moore R, Cosco N. 2010. Using behaviour mapping to investigate healthy outdoor environments for children and families: conceptual framework, procedures and application. In: Thompson CW, Aspinall P, Bell S, editors. Innovative approaches to researching landscape and health. London: Routledge (http://www.naturalearning.org/sites/default/files/OpenSpace2_Moore_Cosco2010Full.pdf)

Munson B, Martz M, Shimek S. 2013. Scientists' and teachers' perspectives about collaboration. J Coll Sci Teach 43:30–35.

National Research Council. 2000. Inquiry and the National Science Education Standards: a guide for teaching and learning. Washington (DC): The National Academies Press.

Paechter C. 2006. Reconceptualizing the gendered body: learning and constructing masculinities and femininities in school. Gend Educ 18:121–35.

Roberts J. 2015. Experiential education in the college context: what it is, how it works, and why it matters. Abingdon: Routledge.

Russell B. 1990. The problems of philosophy. Indianapolis (IN): Hackett Pub. Co.

Schwartz DL, Martin T. 2004. Inventing to prepare for future learning: the hidden efficiency of encouraging original student production in statistics instruction. Cogn Instr 22:129–84.

Singer SR, Nielsen NR, Schweingruber HA. 2012. Discipline-based education research: understanding and improving learning in undergraduate science and engineering. Washington (DC): National Academies Press.

Stine S. 1997. Landscapes for learning: creating outdoor environments for children and youth. Indianapolis (IN): Wiley Press.

van Uum M, Verhoeff R, Peeters M. 2016. Inquiry-based science education: towards a pedagogical framework for primary school teachers. Int J Sci Educ 38:450–69.

Weisberg SM, Newcombe NS. 2017. Embodied cognition and STEM learning: overview of a topical collection in CR: pI. Cogn Res 2:38 (doi: 10.1186/s41235-017-0071-6).

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 140–149
doi:10.1093/icb/icy009

Society for Integrative and Comparative Biology

SYMPOSIUM

On the Cutting Edge of Research to Conserve At-Risk Species: Maximizing Impact through Partnerships

Shauna R. Marquardt,[1,*] Mandy Annis,[†] Ryan G. Drum,[‡] Stephanie Longstaff Hummel,[‡] David E. Mosby[*] and Tamara Smith[§]

[*]Missouri Ecological Services Field Office, U.S. Fish and Wildlife Service, Columbia, MO 65202, USA; [†]Michigan Ecological Services Field Office, U.S. Fish and Wildlife Service, East Lansing, MI 48823, USA; [‡]Midwest Regional Office, U.S. Fish and Wildlife Service, Bloomington, MN 55437, USA; §Minnesota-Wisconsin Ecological Services Field Office, U.S. Fish and Wildlife Service, Bloomington, MN 55425, USA

From the symposium "Science in the Public Eye: Leveraging Partnerships" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1]E-mail: shauna_marquardt@fws.gov

Synopsis Today's conservation challenges are complex. Solving these challenges often requires scientific collaborations that extend beyond the scope, expertise, and capacity of any single agency, organization, or institution. Conservation efforts can benefit from interdisciplinary collaboration, scientific and technological innovations, and the leveraging of capacity and resources among partners. Here we explore a series of case studies demonstrating how collaborative scientific partnerships are furthering the mission of the US Fish and Wildlife Service (USFWS), including: (1) contaminants of emerging concern in the Great Lakes Basin, (2) Poweshiek skipperling conservation, (3) using technology to improve population survey methods for bats and monarch butterfly, and (4) Big River restoration in the Southeast Missouri lead mining district. These case studies illustrate how strategic and effective scientific collaboration is a multi-stage process that requires investment of time and resources by all participants. Early coordination and communication is crucial to aligning planned work with scientific and decision-making needs. Collaborations between USFWS and external scientists can be mutually beneficial by supporting the agency mission while also providing an avenue for innovative research to be directly applied in conservation decisions and management actions.

Introduction

The US Fish and Wildlife Service (USFWS) manages National Wildlife Refuges, protects and recovers endangered species, manages migratory birds, conserves nationally significant fisheries, and enforces federal wildlife laws. Many of the conservation challenges faced by the USFWS necessitate active engagement of stakeholders and scientific experts to achieve the agency mission. Notably, the agency mission of the USFWS—working with others to conserve, protect, and enhance fish, wildlife, and plants and their habitats for the continuing benefit of the American people—emphasizes the involvement of partners in the conservation of the nation's natural resources.

All USFWS programs have a role in accomplishing the agency mission. Programs such as Ecological Services, Migratory Birds, and Fish and Aquatic Conservation do so through implementation of policy, development of conservation and restoration strategies, restoration and protection of habitats and species, and evaluation of the success of conservation actions and strategies. There is a scientific basis to all of these activities. Whereas the USFWS workforce maintains a wide breadth of scientific expertise, the agency does not house experts in all necessary fields to address all possible complex and emerging conservation issues and thus often relies on external scientists to serve as technical experts (USFWS 1994). Furthermore, conservation and

Advance Access publication April 25, 2018
Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology 2018.

recovery efforts often benefit from input from diverse perspectives and skill sets offered by a combination of agency and external scientists (Asquith 2001; Boersma et al. 2001; Gerber and Schultz 2001; Stinchcombe et al. 2002).

The responsibility of the USFWS to inform policy, conservation strategy, and management decisions with sound science makes collaboration with external scientists instrumental to accomplishing effective conservation. Additionally, many opportunities exist for external scientists to proactively engage the USFWS as a means to move their work from theory to practice. A more complete understanding by academic scientists and students of the breadth of opportunities to interface with agency scientists and subsequent adoption of an effective approach for developing collaborative science partnerships can lead to increased visibility and relevancy of their work to the public.

Engagement with external scientists

The USFWS interfaces in multiple ways with scientists from numerous sectors of the conservation field, including academic institutions, non-governmental organizations, state agencies, tribes, and other federal agencies. Modes of engagement with external scientists can vary from relatively brief collaborations, which can include data collection exercises, information sharing through meetings, and participation in webinars on topics of mutual interest, to more formalized and complex partnerships focused on developing conservation strategies or original research. In this discussion we distinguish formal or informal collaborative science partnerships from general collaborative activities with external scientists based on a longer duration, shared objectives, and higher level of resource investment by all parties.

Collaboration for data collection refers to compiling existing empirical and anecdotal data as well as eliciting and incorporating knowledge and opinion from subject matter experts. Data collection is accomplished through participatory exercises such as working groups and structured expert elicitation. Working groups are formed to address specific conservation issues or prioritization needs through interactive discussions, strategy development, and product creation. The membership of working groups typically includes individuals who are experts in species biology, specialists in applicable laboratory or field methodologies, members of diverse stakeholder groups, and specialists that bring to the effort interdisciplinary and technical skills that are value-added for addressing the issue at hand.

Expert elicitation is a data collection process that enables the inclusion of expert opinion and professional judgment while reducing bias, quantifying uncertainty, and allowing for peer review through structured processes (Burgman et al. 2011; Martin et al. 2012; Drescher et al. 2013). Use of expert knowledge is advantageous, or even essential, when empirical data are lacking either because complex conservation issues have not been thoroughly studied or there is an imminent need to understand and act on emerging conservation issues. The latter is often the case when addressing threats to imperiled species. For example, structured expert elicitation has been used in the conservation of at-risk species to rank threats (Donlan et al. 2010), evaluate impacts from specific threats (Frick et al. 2017), and provide parameters to inform demographic population models (Oberhauser et al. 2016).

Collaborative science partnerships between the USFWS and external scientists differ from data collection exercises in that they result in generation of data, techniques, and relevant knowledge to further the conservation of federally protected species, at-risk species, or their habitats, as well as to inform restoration and management efforts. Projects can be undertaken to address priority information needs identified by working groups or during expert elicitation, or they can be developed independently by agency biologists and collaborators. Agency scientists and collaborators work together to understand conservation issues, define project goals and objectives, identify useful products and science delivery tools, convene teams of scientists with the expertise to achieve project goals, and secure sufficient financial and logistical support for project implementation.

The USFWS invests in priority science initiatives through allocation of funding and in-house scientific expertise. For example, the USFWS has allocated $40 million since 2008 to fund bat and white-nose syndrome (WNS) related surveillance and monitoring, research, and management activities. This includes $30 million in grants to other federal, state, provincial, and non-governmental agencies (https://www.whitenosesyndrome.org/research-monitoring). Additionally, since 2010, the USFWS has managed more than $256 million in funds from the Great Lakes Restoration Initiative (GLRI), both to directly implement conservation as well as to collaborate with partners to address data gaps and evaluate environmental conditions.

In addition to funding provided by the agency to support collaborative science initiatives, USFWS scientists actively engage with partners in studies and data analyses to understand species biology, evaluate threats, and develop new techniques and tools. Recent collaborative projects completed in the Midwest Region of the USFWS involving agency scientists include work on: identification and assessment of threats to federally listed and at-risk species and their habitats (ThogMartin et al. 2012a, 2012b, 2013, 2017b; Erickson et al. 2016; Daniel et al. 2017; Strobel and Giorgi 2017); habitat conservation actions (Thogmartin et al. 2017a); adaptive management strategies for federally listed species (Moore et al. 2011); species ecology and distribution (Russell et al. 2014; Clymer and Blanchong 2016); impacts of environmental contaminants on wildlife and natural systems (Simon and Morris 2009; Weber et al. 2015; Simon et al. 2013; Eidels et al. 2016); and large-scale prioritization of conservation actions (Januchowski-Hartley et al. 2013; Daniel et al. 2017).

Considerations for developing partnerships

Establishing strategic science partnerships requires an investment of time and resources by all partners and a clear understanding of expectations, goals, resources, and modes of delivery. The early stages of partnership development can be conceptualized as a stepwise process, although the progression is rarely truly linear or the steps strictly sequential. Viewing the process as steps (Fig. 1) ensures that consideration is given to all stages and allows emphasis to be placed on pivotal components as appropriate, such as early communication with resource managers.

The early stages of development, while vital to the overall success of the partnership, can be undervalued and overlooked. For example, it is during the stage of Initial Coordination that agency scientists and external collaborators can engage in active dialog to ensure that future work is relevant to current conservation issues and useful to conservation practitioners. Such early communication facilitates well-aligned research that minimizes the research-implementation gap (Knight et al. 2008) and maximizes the likelihood that research will have an instrumental impact directly influencing policy development, regulatory decisions, or deployment of conservation resources (Rudd et al. 2011; Rudd 2011).

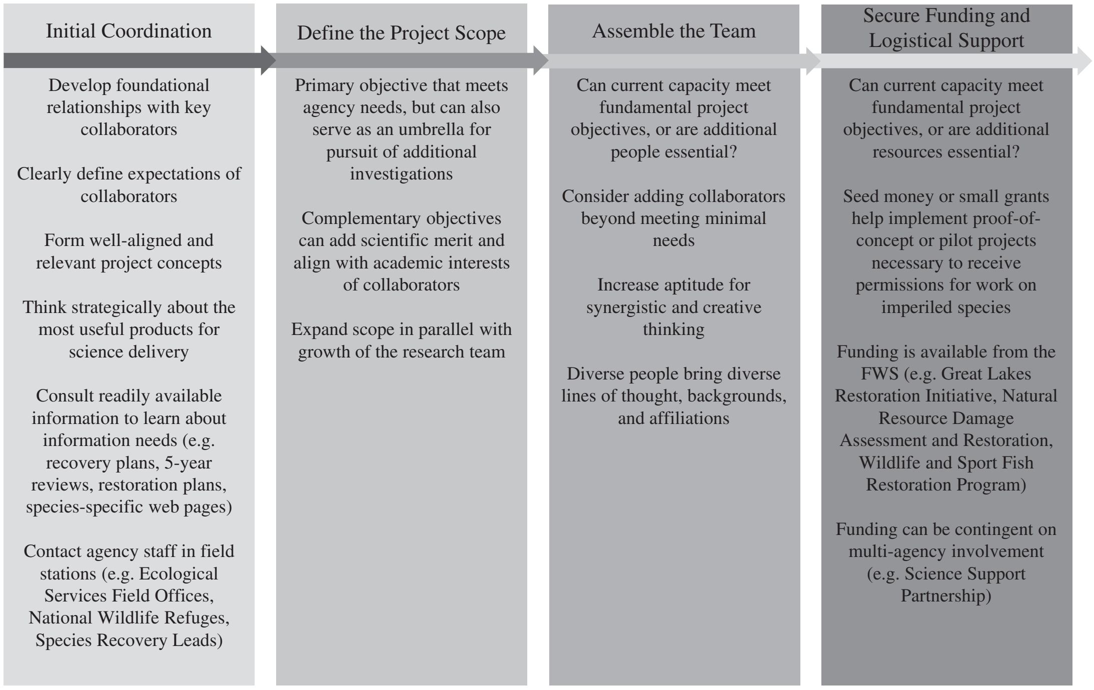
Case studies of collaborative science partnerships

To illustrate the USFWS's engagement in interdisciplinary science partnerships that facilitate achievement of the agency mission, we present case studies from the Midwest Region of the USFWS. The case studies highlight some of the contemporary conservation issues faced by the USFWS giving insight into the breadth of the agency's science needs and providing examples of various ways that external scientists have interfaced with agency scientists. Additionally, the case studies demonstrate how effective, mutually beneficial partnerships directly inform resource management because of deliberative and strategic approaches to development.

Contaminants of emerging concern in the Great Lakes Basin

The GLRI, launched in 2010, provides guidance and support for actions to help restore and sustain the health of the Great Lakes ecosystem in the Upper Midwest of the United States (https://www.glri.us/). One focus of GLRI is to identify potential impacts to fish and wildlife from contaminants of emerging concern (CECs), including pharmaceuticals, personal care products, and new agricultural and industrial chemicals, and their byproducts. CECs are ubiquitous throughout the Great Lakes, yet in 2010 little was known about their extent and impacts (Choy et al. 2013; Elliott et al. 2017).

Biologists from USFWS partnered with other federal and state agencies, academia, and independent specialists to understand the extent of CEC contamination (Phase I 2010–2015) and impacts to natural resources (Phase II 2015–2020) in order to manage and sustain natural resources for current and future generations. Collaborations among federal agencies (e.g., USFWS, US Environmental Protection Agency [EPA], US Geological Survey [USGS], US Army Corps of Engine ers, and National Oceanic and Atmospheric Administration) have created an opportunity to leverage limited resources, harness individual expertise, and address each agency's mandates while achieving mutual goals. In addition to contributing to the integrated work among federal agencies, USFWS is specifically assessing population-level impacts of CECs to USFWS trust resources including fish, migratory birds, and threatened and endangered (T/E) species. Collaborative work includes ongoing field and laboratory studies to assess how CECs affect reproduction and fitness of various taxa (Thomas et al. 2017; Jorgenson et al. 2018): fish with St. Cloud State University, St. Thomas University, Michigan Department of Natural Resources, and Wisconsin Department of Natural Resources; freshwater mussels with Central Michigan University; and birds with Dr. James Ludwig. Initial studies focused on common species, but new techniques are being developed to allow non-lethal sampling and modeling to assess T/E



Initial Coordination	Define the Project Scope	Assemble the Team	Secure Funding and Logistical Support
Develop foundational relationships with key collaborators Clearly define expectations of collaborators Form well-aligned and relevant project concepts Think strategically about the most useful products for science delivery Consult readily available information to learn about information needs (e.g. recovery plans, 5-year reviews, restoration plans, species-specific web pages) Contact agency staff in field stations (e.g. Ecological Services Field Offices, National Wildlife Refuges, Species Recovery Leads)	Primary objective that meets agency needs, but can also serve as an umbrella for pursuit of additional investigations Complementary objectives can add scientific merit and align with academic interests of collaborators Expand scope in parallel with growth of the research team	Can current capacity meet fundamental project objectives, or are additional people essential? Consider adding collaborators beyond meeting minimal needs Increase aptitude for synergistic and creative thinking Diverse people bring diverse lines of thought, backgrounds, and affiliations	Can current capacity meet fundamental project objectives, or are additional resources essential? Seed money or small grants help implement proof-of-concept or pilot projects necessary to receive permissions for work on imperiled species Funding is available from the FWS (e.g. Great Lakes Restoration Initiative, Natural Resource Damage Assessment and Restoration, Wildlife and Sport Fish Restoration Program) Funding can be contingent on multi-agency involvement (e.g. Science Support Partnership)

Fig. 1 Partnership development is a cyclical, adaptive process, but the early stages can be viewed in a stepwise manner to facilitate thorough consideration of foundational elements. Communication and engagement between collaborators and USFWS scientists at each stage, from project conceptualization to acquisition of resources, serves to maximize mutual benefits and likelihood of successful implementation.

species. USFWS and partners are using empirical data from laboratory and field studies to evaluate CEC sensitivity, including chemical characterization with Southern Illinois University and cell receptor sensitivity with St. Cloud State University. Modeling exercises are being conducted by the University of Minnesota and Ball State University to validate CEC population impacts, and by USGS to validate watershed hazard assessments by evaluating the presence and occurrence of CECs throughout the Great Lakes Basin.

USFWS will use results from the suite of studies to inform resource management decisions by providing sublethal population-level assessments of CEC risks to trust resources, including T/E species. Preliminary results suggest that CECs are contributing to sublethal effects on fish and may lead to population-level declines (Thomas et al. 2017; Jorgenson et al. 2018). Results will be disseminated through outreach to federal, state, tribal, and local natural resource managers and the public. In addition, federal agencies will produce an Integrated Report assessing CEC impacts that provide management recommendations in 2020. Further, USFWS and collaborators are producing peer-reviewed articles for technical audiences. With limited resources, it is more important than ever for resource managers to understand the stressors which may impact vulnerable species populations to help prioritize areas best suited for restoration and conservation efforts. These studies will provide information regarding potential population-level impacts of CECs enabling managers to select optimal conservation and management practices in order to avoid further population declines, future listing of imperiled species, and loss of trust resources for the continued benefit of current and future generations.

Lessons learned—GLRI exemplifies how a large, well-coordinated partnership can address complex, large scale conservation issues to achieve the missions of multiple agencies. Implementation of a restoration project with a broad scope requires scientific expertise of equivalent breadth that is harnessed through continuous coordination and clearly defined goals, objectives, and actions. The initiative has been successful through assembly and engagement of numerous, appropriate agencies, and organizations while still capitalizing on the expertise of individual scientific experts. Whereas coordination can present challenges, engagement of an extensive suite of collaborators has maximized the cumulative financial and logistical capacity that has been brought to bear. The success of GLRI has hinged on mutual investment of time, human capital, and tangible resources.

Poweshiek skipperling conservation strategy

Until recently, the Poweshiek skipperling (*Oarisma poweshiek*), a small butterfly that occurred historically in tallgrass prairie and prairie fens, was regarded as "the most frequently and reliably encountered of the prairie-obligate skippers" in the Upper Midwest, but now faces a high risk of extinction (Dana 2008). This species is now known only from approximately 1% of the sites where it previously occurred in Wisconsin and Michigan, USA, and Manitoba, Canada. The USFWS listed the Poweshiek skipperling as endangered under the Endangered Species Act (16 U.S.C. 1531 *et seq.*) (ESA) in 2014 (USFWS 2014). A multi-agency partnership was created in 2015 to develop a conservation strategy for the Poweshiek skipperling, the basis of which would be development of protocols to facilitate captive rearing, augmentation of existing populations, and, eventually, reintroduction of the species to sites within its historical range (Smith et al. 2016; USFWS 2016, 2017).

The USFWS convened a workshop with partnering agencies and researchers in October, 2015, at the Minnesota Zoo, Apple Valley, Minnesota, USA, to assess *ex situ* rearing as a conservation tool for Poweshiek skipperling. Scientists with the International Union for the Conservation of Nature (IUCN) Species Status Commission (SSC) Conservation Breeding Specialist Group (CBSG) facilitated the workshop in which the group of scientists provided data, professional opinion, and biological expertise on potential recovery tools. Experts recommended a strategy that incorporated both short-term and long-term measures, including a head-start program, surrogate research using the closely related Garita skipper (*O. garita*), and an insurance population program (Delphey et al. 2016; Smith et al. 2016). A suite of collaborators are conducting complementary research on breeding and husbandry techniques, larval host preferences, and pesticide tolerance using closely related species to support *ex situ* management. Additional research projects on habitat restoration and pesticide risk assessments are occurring at extant and potential reintroduction sites to determine suitability for reintroductions.

Development of complex conservation and recovery strategies requires cooperation between the USFWS, State of Michigan, Michigan Natural Features Inventory, Springfield Township in Michigan, Minnesota Zoo, The Nature Conservancy (TNC) of Canada, Assiniboine Park Zoo, Central Michigan University, University of Winnipeg, Minnesota Department of Natural Resources, Minot University, Milwaukee Public Museum, Wisconsin Department of Natural Resources, New College of Florida, independent researchers, and private landowners. The Poweshiek Skipperling Conservation Strategy project is in its second year (Smith et al. 2016). After 5 years, USFWS biologists will evaluate captive rearing and reinforcement actions by comparing population trends post-release to trends observed from 2011 to 2016. They also will evaluate survival from egg to release while in captivity to determine whether it is likely to exceed an estimated 3% survival rate in the wild, based on that of another rare butterfly (Lambert 2011).

The USFWS and partners will take immediate action to prevent the extinction of the Poweshiek skipperling by augmenting populations at two to three sites using head-started, captive-reared individuals (Smith et al. 2016). This action is intended to stabilize declining population trends and increase growth rates of current populations through reinforcement and protection of populations and will be supported with appropriate habitat management (Smith et al. 2016; USFWS 2016, 2017). The ultimate goal of the Poweshiek Skipperling Conservation Strategy project is recovery of the species according to measureable criteria defined in the reintroduction and propagation plan (Smith et al. 2016), the conservation strategy (USFWS 2016), focal species action plan (USFWS 2017), and in the future recovery plan (in development).

Lessons learned—The effort for Poweshiek skipperling recovery demonstrates how input from external scientists is included in multiple stages of imperiled species recovery programs, from workshops with experts to identify conservation actions to targeted research on key aspects of biology and threats. Because agency and external scientists worked together during the initial coordination stage of project development, the scope of research being undertaken is well-defined and highly relevant to implementation of the overall conservation strategy. The effort involves the agency scientists responsible for coordinating the program as well as experts from academia and conservation organizations who are intimately familiar with the species' biology. Success of the partnership is further demonstrated through the development of innovative techniques and approaches that are being applied to the Poweshiek skipperling as well as other imperiled grass skippers (Delphey et al. 2017; Runquist and Nordmeyer 2018).

Counting bats and butterflies using LiDAR

Bats and butterflies may seem to have relatively little in common. Yet scientists who need to quantify their numbers face similar challenges. The USFWS uses data on status and trends for populations of imperiled species to evaluate threats, make listing decisions, and develop recovery plans and recovery criteria. Traditional approaches to quantify populations tended to rely on census measures, sampling, and statistical techniques to infer an estimate of population size. However, some species are particularly difficult to count due to unique behaviors, detection challenges, environmental conditions, and sheer numbers. Gregarious hibernating bats and monarch butterflies (*Danaus plexippus*) overwinter in large numbers in highly dense, three-dimensional clusters presenting the opportunity to measure populations when they congregate during their overwintering seasons.

The gray myotis (*Myotis grisescens*) and Indiana myotis (*M. sodalis*) are two of the seven federally listed bat species in the United States. Many decisions about conservation efforts and recovery status of these species are based on winter survey data acquired while bats are hibernating in caves and mines (e.g., USFWS 1982, 2007). Traditional survey methods of hibernating populations, which can number in the thousands or hundreds of thousands, are plagued with biases because of irregularities in substrate, roosting behavior, and low repeatability among survey years, and have the potential to cause excessive disturbance (Thomas and LaVal 1988). The level of disturbance caused to hibernating bats coupled with the high uncertainty of traditionally acquired estimates necessitates a reevaluation of methodologies and modern technological tools have shown promise as an alternative (Azmy et al. 2012; McFarlane et al. 2015; Shazali et al. 2017).

Similarly, overwintering sites for monarch butterflies in high-elevation forests of central Mexico hold upward of 10 million or more monarchs clustered over the surface of a few trees (Urquhart and Urquhart 1976; Brower 1977). Since the early 1990s, efforts to estimate populations have been led by World Wildlife Fund-Mexico, in collaboration with the Mexican Secretariat of Environment and Natural Resources (Secretaría de Medio Ambiente y Recursos Naturales), the National Commission for Protected Areas (Comisión Nacional de Áreas Naturales Protegidas), and the Monarch Butterfly Biosphere Reserve. Biologists have used the occupied surface area of the colonies, a hectare-based estimate, as an index of population size (Rendón-Salinas and Tavera-Alonso 2014). Various methods have been attempted to count individual overwintering monarchs, including capture–mark–recapture techniques (Calvert 2004), netting and removal of occupied branches from trees (Calvert 2004), and drawing inferences from storm mortality events (Brower et al. 2004). Still, a 95% credible interval ranging between 2.4 and 80.7 million monarchs per hectare indicates that much uncertainty remains regarding absolute numbers (Thogmartin et al. 2017c).

Recognizing the potential benefits from a parallel, collaborative approach, USFWS scientists initiated a unique, interdisciplinary partnership to leverage resources and expertise, and explore technological solutions to address a common problem between bats and butterflies. Currently, efforts are underway to use Light Detection and Ranging (LiDAR)—laser-based tools for measuring three-dimensional structures—and other technological approaches to estimate population sizes. In partnership with the Center for Design Innovation, Winston-Salem State University, TERC, and the USGS, a team of biologists, quantitative ecologists, engineers, and outreach specialists are drawing from tools typically used in the fields of architecture or historical preservation to explore new methods to quantify the volume occupied by overwintering bats and monarchs, which can then be used to estimate abundance. Results will directly inform the conservation and management of imperiled bats and monarch butterflies and will be communicated to the public through traditional scientific channels as well as through outreach tools and programs targeted to a broader audience.

Lessons learned—The foundational relationships that have facilitated the notably swift and innovative work of this partnership were developed during initial coordination. Early coordination and transparent communication between agency and external scientists served to clearly define expectations of all partners and identify desired outcomes and products. The progression of development of the bats and butterflies LIDAR project also illustrates the non-linear, often cyclical process of project development, with the scope evolving as more diverse expertise and creative lines of thought are introduced to the team. In this case, the original project that focused on hibernating bats was expanded to include monarch and effectively maximized the efficient use of resources, breadth of scientific capacity, and overall conservation impact.

Big river restoration in the southeast Missouri lead mining district

In the Big River and Meramec River watersheds of the southeast Missouri Ozarks, the largest historic lead mining district in the United States intersects with one of the most diverse aquatic riverine ecosystems in the Upper Mississippi Basin with some unfortunate results. Researchers through the decades have documented impacts to aquatic biota, including mussels, associated with heavy metal contaminated sediments. The Old Lead Belt, which drains into the Big River in southeast Missouri, produced several millions of tons of mine and mill waste that have eroded into the Big River and its tributaries since the mid-1800s. Of specific concern to the USFWS are four federally listed mussel species that contribute to the diversity of the area. This unfortunate circumstance for benthic biota has been a rich setting for the USFWS, other agencies, and researchers have collaborated on research to understand the extent of impacts and restore habitats necessary to support aquatic organisms.

Modern scientific investigations of lead impacts began in the Big River in the late 1970s after a storm event caused a large scale release of lead mill waste (approximately 50,000 cubic meters) into the river. Early research by the Missouri Department of Conservation (MDC) and USFWS investigated distribution of freshwater mussels and uptake of heavy metals in mussels and other benthic biota following this event (Buchanan 1980; Schmitt and Finger 1982; Czarnezki 1985). Based on threats to human health identified through the investigation, the Missouri Department of Health and Senior Services (MDHSS) issued an advisory against consuming certain benthic fish species for over 170 km of the Big River. Furthermore, researchers documented toxic levels of lead-contaminated sediment in the Big River that extend over 170 km to its confluence with the Meramec River (Schmitt and Finger 1982; Roberts et al. 2010; Pavlowsky et al. 2017). Identification of the severity and extent of impairment to the river were a springboard for developing a partnership between federal and state agencies, academic institutions, contractors for the mining companies, and TNC.

A suite of collaborative research projects contributing to the Big River restoration effort were undertaken as part of a Natural Resource Damage Assessment of the area. A major focus of the assessment was to determine which benthic organisms were adversely affected by metal toxicity versus adverse effects from other habitat factors such as excessive sediment load, point source discharge, and agricultural or urban land use. From 2008 to 2017 scientists from USFWS, USGS, MDC, Missouri Department of Natural Resources, Missouri State University, and University of Missouri designed and implemented cohesive and complementary studies to identify impacts to mussels, crayfish, riffle-dwelling fish; document the extent of contamination in sediment and the floodplain; and identify drivers of mussel distribution. One such series of consecutive studies included a quantitative evaluation by USFWS of mussel populations and correlations with sediment contamination, a USGS evaluation of toxicity to juvenile mussels and amphipods from sediments collected from the same locations as a field evaluation conducted by USFWS (Besser et al. 2009; Roberts et al. 2010); an evaluation by USGS and MDC of impacts to crayfish density and *in situ* toxicity (Allert et al. 2009; McKee et al. 2010); an evaluation by USGS and USFWS of habitat factors that dictate freshwater mussel distribution (Albers et al. 2016; Roberts et al. 2016); and documentation of the longitudinal and vertical extent of sediment contamination in stream and floodplains by researchers at Missouri State University (Pavlowsky et al. 2017). Ultimately, the purpose of all investigations is to inform clean-up decisions and restoration methods beneficial to mussels and other aquatic life in the Big River and Meramec River basins.

Lessons learned—Partnership development for the Big River Restoration Project followed an ideal progression through the stages of collaborative definition of the project scope, assembling the necessary team of scientists, and pooling resources to ensure that research goals and objectives were met. Because of the extensive scope of work to be completed, once collaborators identified and prioritized research needs, individual projects, or activities within a project, were completed by agency or academic scientists with the appropriate expertise and resources. The approach maintains a focus on injury assessment and restoration for the purposes of the Natural Resource Damage Assessment, yet provides information that will inform clean-up decisions for EPA, and provides sufficient flexibility for external scientists to engage in aspects of the effort that meet their academic interests.

Conclusions

Effective, science-driven conservation is accomplished through strategic partnerships and continuously evolving collaborations. Case studies from the Midwest Region of the USFWS are a small representation of the wide breadth of investigations and analyses occurring across the agency that would not be possible without engagement of diverse external scientists. These case studies also illustrate how attention to key stages of partnership development can result in relevant, well-aligned research. Partnerships between USFWS and external scientists can be viewed as mutually beneficial in that they facilitate accomplishment of the agency mission while providing an avenue for innovative research to have a direct influence on conservation decisions.

Acknowledgments

We thank L. Williams, A. Trowbridge, M. Merson, and L. Morgan for review and feedback on the manuscript. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the USFWS.

Funding

Funding was provided from the Great Lakes Restoration Imitative through the U.S. Fish and Wildlife Service Region 3 Ecological Services Program.

References

Albers JL, Besser JM, Schmitt CJ, Wildhaber ML. 2016. Mussel Community Associations with Sediment Metal Concentrations and Substrate Characteristics in the Big River, Missouri, USA: Administrative Report to the U.S. Fish and Wildlife Service. Columbia Environmental Research Center, Columbia (MO): U.S. Geological Survey. p. 1–82.

Allert AL, DiStefeno RJ, Fairchild JF, Schmitt CJ, Brumbaugh WG. 2009. Effects of mining-derived metals on riffle-dwelling crayfish and in-situ toxicity to juvenile *Orconectes hylas* and *Orconectes luteus* in the Big River of southeast Missouri, USA: Administrative Report to the U.S. Fish and Wildlife Service. Columbia Environmental Research Center, Columbia (MO): U.S. Geological Survey. p. 1–90.

Asquith NM. 2001. Misdirections in conservation biology. Conserv Biol 15:345–52.

Azmy SN, Sah SAM, Shafie NJ, Ariffin A, Majid Z, Ismail MNA, Shamsir MS. 2012. Counting in the dark: non-intrusive laser scanning for population counting and identifying roosting bats. Sci Rep 2:254 (doi: 10.1038/srep00524).

Besser JM, Brumbraugh WG, Hardesty DK, Hughes JP, Ingersoll CG. 2009. Assessment of Metal-Contaminated Sediments from the Southeast Missouri (SEMO) Mining District using Sediment Toxicity Tests with Amphipods and Freshwater Mussels: Administrative Report, 08-NRDAR-02. Columbia Environmental Research Center, Columbia (MO): U.S. Geological Survey. p. 1–59.

Boersma PD, Kareiva P, Fagan WF, Clark JA, Hoekstra JM. 2001. How good are endangered species recovery plans? BioScience 51:643–9.

Brower LP. 1977. Monarch migration. Nat Hist 86:40–53.

Brower LP, Kust DR, Rendón-Salinas E, García-Serrano E, Kust KR, Miller J, Fernandez del Rey C, Pape K. 2004. Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. In: Oberhauser KS, Solensky MJ, editors. The monarch butterfly: biology and conservation. Ithaca: Cornell University Press. p. 151–66.

Buchanan AC. 1980. Mussels (Naiades) of the Meramec River basin, Missouri. Missouri Department of Conservation Aquatic Series No. 17. p. 1–76.

Burgman M, Carr A, Godden L, Gregory R, McBride M, Flander L, Maguire L. 2011. Redefining expertise and improving ecological judgment. Conserv Lett 4:81–7.

Calvert WH. 2004. Two methods estimating overwintering monarch population size in Mexico. In: Oberhauser KS, Solensky MJ, editors. The monarch butterfly: biology and conservation. Ithaca: Cornell University Press. p. 121–7.

Choy SJ, Annis ML, Banda JA, Bowman SR, Brigham ME, Elliott SM, Gefell DJ, Jankowski MD, Jorgenson ZG, Lee KE, et al. 2013. Contaminants of Emerging Concern in the Great Lakes Basin: A Report on Sediment, Water, and Fish Tissue Chemistry Collected in 2010–2012. Michigan Ecological Services Field Office, Lansing (MI): U.S. Fish and Wildlife Service. p. 1–90.

Clymer J, Blanchong J. 2016. Iowa Northern Long-Eared Bat Acoustic Monitoring: Final Report, 2016. Ames (IA): Iowa State University. p. 1–91.

Czarnezki JM. 1985. Accumulation of lead in fish from Missouri streams impacted by lead mining. Bull Environ Contam Toxicol 34:736–45.

Dana R. 2008. Southwest Minnesota prairie Lepidoptera study, 2007—Draft. Minnesota County Biological Survey, St. Paul (MN): Minnesota Department of Natural Resources. p. 1–35.

Daniel W, Sievert N, Infante D, Whittier J, Stewart J, Paukert C, Herreman K. 2017. A decision support mapper for conserving stream fish habitats of the Northeast Climate Science Center region: Final Report, 2017. Missouri Cooperative Fish and Wildlife Research Unit, Columbia (MO): U.S. Geological Survey. p. 1–10.

Delphey P, Runquist E, Harris T, Nordmeyer C, Smith T, Traylor-Holzer K, Miller PS. 2016. Poweshiek Skipperling and Dakota Skipper: Ex Situ Feasibility Assessment and Planning Workshop: Final Report. Apple Valley (MN): IUCN/SSC Conservation Breeding Specialist Group. p. 1–128.

Delphey P, Runquist E, Nordemeyer C. 2017. Plan for the Controlled Propagation, Augmentation, and Reintroduction of Dakota skipper (Hesperia dacotae)—Draft. Bloomington (MN): U.S. Fish and Wildlife Service. p. 1–60.

Donlan CJ, Wingfield DK, Crowder LB, Wilcox C. 2010. Using expert opinion surveys to rank threats to endangered species: a case study with sea turtles. Conserv Biol 24:1586–95.

Drescher M, Perera AH, Johnson CJ, Buse LJ, Drew CA, Burgman MA. 2013. Toward rigorous use of expert knowledge in ecological research. Ecosphere 4:art83–26.

Eidels RR, Sparks DW, Whitaker, Jr JO, Sprague CA. 2016. Sub-lethal effects of chlopyrifos on big brown bats (*Eptesicus fuscus*). Arch Environ Contam Toxicol. 71:322–335.

Elliott SM, Brigham ME, Lee KE, Banda JA, Choy SJ, Gefell DJ, Minarik TA, Moore JN, Jorgenson ZG. 2017. Contaminants of emerging concern in tributaries to the

Laurentian Great Lakes: i. Patterns of occurrence. PLoS One 12:e0182868 (doi: 10.1371/journal.pone.0182868).

Erickson RA, Thogmartin WE, Diffendorfer JE, Russell RE, Szymanski JA. 2016. Effects of wind energy generation and white-nose syndrome on the viability of the Indiana bat. PeerJ 4:e2830 (doi:10.7717/peerj.2830).

Frick WF, Baerwald EF, Pollock JF, Barclay RMR, Szymanski JA, Weller TJ, Russell AL, Loeb SC, Medellin RA, McGuire LP. 2017. Fatalities at wind turbines may threaten population viability of a migratory bat. Biol Conserv 209:172–7.

Gerber LR, Schultz CB. 2001. Authorship and the use of biological information in endangered species recovery plans. Conserv Biol 15:1308–14.

Januchowski-Hartley SR, McIntyre PB, Diebel M, Doran PJ, Infante DM, Joseph C, Allan JD. 2013. Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and road crossings. Front Ecol Environ 11:211–7.

Jorgenson ZG, Thomas LM, Elliott SM, Cavallin JE, Randolph EC, Choy SJ, Alvarez DA, Banda JA, Gefell DJ, Lee KE, et al. 2018. Contaminants of emerging concern presence and adverse effects in fish: a cast study of the Laurentian Great Lakes. Environ Pollut 236:718–33.

Knight AT, Cowling RM, Rouget M, Balmford A, Lombard AT, Campbell BM. 2008. Knowing but not doing: selecting priority conservation areas and the research-implementation gap. Conserv Biol 22:610–7.

Lambert AM. 2011. Natural history and population ecology of a rare pierid butterfly, Euchloe ausonides insulanus Guppy and Shepard (Pieridae) [dissertation]. [Ann Arbor (MI)]: University of Washington.

Martin TG, Burgman MA, Fidler F, Kuhnert PM, Low-Choy S, McBride M, Mengersen K. 2012. Eliciting expert knowledge in conservation science. Conserv Biol 26:29–38.

McFarlane DA, Roberts W, Buchroithner M, Van Rentergem G, Lundberg J, Hautz S. 2015. Terrestrial LiDAR-based automated counting of swiflet nests in the caves of Gomantong, Sabah, Borneo. Int J Speleol 44:191–5.

McKee M, Vining I, Sheriff S, Girondo J, Meneau K, Reed M, Brown D, Kluesner S. 2010. Effects of Lead-Zinc Mining on Benthic Fish Density in Riffles of the Big River (Southeast Missouri): Final Report, 2010. Resource Science, Columbia (MO): Missouri Department of Conservation. p. 1–39.

Moore CT, Fonnesbeck CJ, Shea K, Lah KJ, McKenzie PM, Ball LC, Runge MC, Alexander HM. 2011. An adaptive decision framework for the conservation of a threatened plant. J Fish Wildl Manage 2:247–61.

Oberhauser K, Wiederholt R, Diffendorfer JE, Semmens D, Ries L, Thogmartin WE, López-Hoffman L, Semmens B. 2016. A trans-national monarch butterfly population model and implications for regional conservation priorities. Ecol Entomol 42:51–60.

Pavlowsky RT, Lecce SA, Owen M, Martin DJ. 2017. Legacy sediment, lead, and zinc storage in channel and floodplain deposits of the Big River, Old Lead Belt Mining District, Missouri, USA. Geomorphology 299:54–75.

Rendón-Salinas E, Tavera-Alonso G. 2014. Monitoeo de la superficie forestal ocupada por las colonias de hibernación de la mariposa Monarca en diciembre de 2013. World Wildlife Fund-México, Zitácuaro, Michoacán.

Roberts A, Hundley J, Mosby D, Rosenberger A, Bouska KL, Simmons B, Lindner G. 2016. Quantitative survey of freshwater mussels (Unionoidea) and assessment of sediment contamination in the Big River, Missouri: Final Report. Natural Resource Damage Assessment, Columbia Missouri Ecological Services Field Office, Columbia (MO): U.S. Fish and Wildlife Service. p. 1–69.

Roberts AD, Mosby D, Weber J, Besser J, Hundley J, McMurray S, Faiman S. 2010. As assessment of freshwater mussel (Bivalvia: Margaritiferidae and Unionidae) populations and heavy metal sediment contamination in the Big River, Missouri: Final Report. Natural Resource Damage Assessment, Columbia Missouri Ecological Services Field Office, Columbia (MO): U.S. Fish and Wildlife Service. p. 1–110.

Rudd MA. 2011. How research-prioritization exercise affect conservation policy. Conserv Biol 25:860–6.

Rudd M, Beazley K, Cooke S, Fleishman E, Lane D, Mascia M, Roth R, Tabor G, Bakker J, Bellefontaine T, et al. 2011. Generation of priority research questions in inform conservation policy and managmenet at a national level. Conserv Biol 25:476–84.

Runquist E, Nordmeyer C. 2018. Minnesota zoo prairie butterfly conservation program: annual report, 2017. Apple Valley (MN): Minnesota Zoo. p. 1–44.

Russell RE, Tinsley K, Erickson RA, Thogmartin WE, Szymanski J. 2014. Estimating the spatial distribution of wintering little brown bat populations in the eastern United States. Ecol Evol 4:3746–54.

Schmitt CJ, Finger SE. 1982. The dynamics of metals from past and present mining activities in the Big and Black River watersheds, Southeastern Missouri: Final Report for the U.S. Army Corps of Engineers. Project No. DACW43-80-A-0109. Columbia National Fisheries Research Laboratory. Columbia (MO): U.S. Fish and Wildlife Service. p. 1–156.

Shazali N, Chew TH, Shamsir MS, Tingga RCT, Mohd-Ridwan AR, Khan FAA. 2017. Assessing bat roosts using the LiDAR system at Wind ave Nature Reserve in Sarawak, Malaysian Borneo. Acta Chiropterol 19:199–210.

Simon TP, Morris CC. 2009. Biological response signature of oil brine threats, sediment contaminants, and crayfish assemblages in an Indiana watershed, USA. Arch Environ Contam Toxicol. 56:96–110.

Simon TP, Morris CC, Sparks DW 2013. Patterns in stream fish assemblage structure and function associated with a PCB gradient. Arch Environ Contam Toxicol. 65:286–99.

Smith T, Cuthrell D, Runquist E, Delphey P, Dana R, Nordmeyer C, Nail KR, Borkin S, Dandridge T, Harris T, et al. 2016. Plan for the controlled propagation, augmentation, and reintroduction of Poweshiek skipperling (Oarisma poweshiek): a cooperative interagency plan. Bloomington (MN): U.S. Fish & Wildlife Service. p. 1–59.

Stinchcombe J, Moyle LC, Hudgens BR, Bloch PL, Chinnadurai S, Morris WF. 2002. The influence of the academic conservation biology literature on endangered species recovery planning. Conserv Ecol 6:15–25.

Strobel BN, Giorgi GF. 2017. Nest-site selection patterns of coexisting sandhill and whooping cranes in Wisconsin. J Fish Wildl Manage 8:588–95.

Thogmartin WE, Diffendorfer JE, López-Hoffman L, Oberhauser K, Pleasants J, Semmens BX, Semmens D, Taylor OR, Wiederholt R. 2017a. Density estimates of monarch butterflies overwintering in central Mexico. PeerJ 5:e3221 (doi: 10.7717/peerj.3221).

Thogmartin WE, King RA, McKann PC, Szymanski JA, Pruitt L. 2012a. Population-level impact of white-nose syndrome on the endangered Indiana bat. J Mammal 93:1086–98.

Thogmartin WE, King RA, Szymanski JA, Pruitt L. 2012b. Space-time models for a panzootic in bats, with a focus on the endangered Indiana bat. J Wildl Dis 48:876–87.

Thogmartin WE, Sanders-Reed CA, Szymanski JA, McKann PC, Pruitt L, King RA, Runge MC, Russell RE. 2013. White-nose syndrome is likely to extirpate the endangered Indiana bat over large parts of its range. Biol Conserv 160:162–72.

Thogmartin WE, López-Hoffman L, Rohweder J, Diffendorfer J, Drum R, Semmens D, Black S, Caldwell I, Cotter D, Drobney P, et al. 2017b. Restoring monarch butterfly habitat in the Midwestern US: 'all hands on deck'. Environ Res Lett 12:074005 (doi: 10.1088/1748-9326/aa7637).

Thogmartin WE, Wiederholt R, Oberhauser K, Drum RG, Diffendorfer JE, Altizer S, Taylor O, Pleasants J, Semmens D, Semmens B, et al. 2017c. Monarch butterfly population decline in North America: identifying the threatening processes. R Soc Open Sci 4:170760 (doi: 10.1098/rsos.170760).

Thomas LM, Jorgenson ZG, Brigham ME, Choy SJ, Moore JN, Banda JA, Gefell DJ, Minarik TA, Schoenfuss HL. 2017. Contaminants of emerging concern in tributaries to the Laurentian Great Lakes: iI. Biological consequences of exposure. PLoS One 12:e0184725 (doi: 10.1371/journal.pone.0184725).

Thomas DW, LaVal RK. 1988. Survey and census methods. In: Kunz TH, editor. Ecological and behavioral methods for the study of bats. Washington, D.C.: Smithsonian Institution Press. p. 77–87.

Urquhart FA, Urquhart NR. 1976. The overwintering site of the eastern population of the monarch butterfly (*Danaus p. plexippus* Danaidae) in southern Mexico. J Lepid Soc 30:153–8.

U.S. Fish and Wildlife Service [USFWS]. 1982. Gray bat recovery plan. Minneapolis (MN): U.S. Fish and Wildlife Service. p. 1–143.

U.S. Fish and Wildlife Service [USFWS]. 1994. Notice of interagency cooperative policy on recovery plan participation and implementation under the Endangered Species Act. Fed Regist 59:34272.

U.S. Fish and Wildlife Service [USFWS]. 2007. Indiana bat (Myotis sodalis) draft recovery plan: first revision. Fort Snelling (MN): U.S. Fish & Wildlife Service. p. 1–260.

U.S. Fish and Wildlife Service [USFWS]. 2014. Endangered and threatened wildlife and plants; threatened species status for Dakota skipper and endangered species status for Poweshiek skipperling; final rule. Fed Regist 79:63672–748.

U.S. Fish and Wildlife Service [USFWS]. 2016. Partnership for Poweshiek skipperling conservation: Conservation Strategy. Bloomington (MN): U.S. Fish & Wildlife Service. p. 1–2.

U.S. Fish and Wildlife Service [USFWS]. 2017. Focal Species Action Plan for Poweshiek skipperling—draft. Bloomington (MN): U.S. Fish and Wildlife Service. p. 1–9.

Weber JS, Goyne KW, Luxton TP, Thompson AL. 2015. Phosphate treatment of lead-contaminated soil: effects on water quality, plant uptake, and lead speciation. J Environ Qual 44:1127–36.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, pp. 150–160
doi:10.1093/icb/icy032

Society for Integrative and Comparative Biology

SYMPOSIUM

Exposing the Science in Citizen Science: Fitness to Purpose and Intentional Design

Julia K. Parrish,[1,*] Hillary Burgess,[*] Jake F. Weltzin,[†] Lucy Fortson,[‡] Andrea Wiggins[§] and Brooke Simmons[¶]

[*]School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA; [†]U.S. Geological Survey, 12201 Sunrise Valley Drive, Reston, VA 20192, USA; [‡]School of Physics and Astronomy, University of Minnesota, Minneapolis, MN 55455, USA; [§]University of Nebraska at Omaha, 6001 Dodge Street, Omaha, NE 68182, USA; [¶]University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093, USA

From the symposium “Science in the Public Eye: Leveraging Partnerships” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2018 at San Francisco, California.

[1]E-mail: jparrish@uw.edu

Synopsis Citizen science is a growing phenomenon. With millions of people involved and billions of in-kind dollars contributed annually, this broad extent, fine grain approach to data collection should be garnering enthusiastic support in the mainstream science and higher education communities. However, many academic researchers demonstrate distinct biases against the use of citizen science as a source of rigorous information. To engage the public in scientific research, and the research community in the practice of citizen science, a mutual understanding is needed of accepted quality standards in science, and the corresponding specifics of project design and implementation when working with a broad public base. We define a science-based typology focused on the degree to which projects deliver the type(s) and quality of data/work needed to produce valid scientific outcomes directly useful in science and natural resource management. Where project intent includes direct contribution to science and the public is actively involved either virtually or hands-on, we examine the measures of quality assurance (methods to increase data quality during the design and implementation phases of a project) and quality control (*post hoc* methods to increase the quality of scientific outcomes). We suggest that high quality science can be produced with massive, largely one–off, participation if data collection is simple and quality control includes algorithm voting, statistical pruning, and/or computational modeling. Small to mid-scale projects engaging participants in repeated, often complex, sampling can advance quality through expert-led training and well-designed materials, and through independent verification. Both approaches—simplification at scale and complexity with care—generate more robust science outcomes.

Introduction

On December 22, 2014, Virginia started her sixth beached bird survey near Ocean Shores, Washington. Trained only 2 months previously, she was still on the learning curve. In fact, she got a lot of practice that day. Virginia and her survey partner found 425 carcasses in less than a kilometer, and photographed, tagged, and identified all of them. This single survey marked the peak of the largest marine bird mass mortality event ever documented in the Pacific Northwest of the United States (Jones et al. 2018). A documentation only possible because more than 500 trained participants of the BeachCOMBERS, BeachWatch, and COASST beached bird survey programs conducted over 1650 standardized, effort-controlled surveys at 264 sites from Morro Bay, CA to Neah Bay, WA. At the same time, program experts verified carcass identification from the collected evidence (photographs, standard measurements, foot type). Finally, almost 20 scientists, including oceanographers, atmospheric scientists, marine ecologists, veterinary pathologists, and seabird biologists brought their expertise to bear in determining the extent, intensity, and causality of the event. In this story, citizen science and science are synonymous. Is this the norm, or the exception?

Advance Access publication July 2, 2018

In this paper, we examine the attributes of citizen science leading to rigorous and robust science.

We define citizen science as projects in which members of the public engage directly in research developed by or with scientists to address particular questions and/or issues (Irwin 1995; Bonney et al. 2009a). Because the term "citizen" can be politically problematic and the term "volunteer" is not always appropriate, we refer to individuals directly involved in citizen science projects and not including project staff as "participants." Within natural science, fields utilizing citizen science already include: archaeology (Bovy et al. 2016), astronomy (Fortson et al. 2012), biochemistry (Eiben et al. 2012), ecology (Dickinson et al. 2010), geography (Goodchild 2007), geology (Powell et al. 2013), and oceanography (Hays et al. 2005). This diversity might suggest that academic and professional science is broadly accepting of public involvement; however, recent studies indicate that the mainstream scientific community remains skeptical of the public as a trusted source of scientific information (Riesch and Potter 2014; Burgess et al. 2017). In many cases, these misgivings are rooted in the demonstration that non-experts in a citizen science program do not always perform a scientific task (usually data collection) to the standards desired by researchers. Thus, the evidence that some citizen science programs produce high quality data of immediate use to science (e.g., Cooper et al. 2014; Swanson et al. 2016) does not translate into the conclusion that all citizen science programs can.

Defining the goals

Many citizen science projects assert production of data in service to science or resource management as a goal. Theobald et al. (2015) found that 97% of 388 surveyed biodiversity citizen science projects stated their primary goal was to contribute to science and/or advance scientific understanding. However, only 12% of projects had demonstrably contributed to a science-focused peer-reviewed publication (one measure of scientific contribution). Even if this publication rate is underreported due to "cryptic" use of the term citizen science only outside of the abstract and keywords if at all (Cooper et al. 2014), the discrepancy suggests that there may be large differences in what project managers, and research scientists, consider evidence of scientific use. In assessing the potential for bonafide science as an outcome of citizen science, we invoke the concept of fitness to use or fitness to purpose (Juran 1951), or the degree to which the quality-related elements or activities of an organization—here a citizen science project—can result in the declared purpose. Simply put, projects claiming science as a primary goal or "purpose" should adhere to accepted quality standards within science (Wiggins et al. 2018).

However, science is not the only goal of citizen science. Other common goals include education, community empowerment, and personal fulfillment. Science education and/or increasing science literacy has long been a major thrust of citizen science programming (Bonney et al. 2009b; Wiggins and Crowston 2011). Community goals, often related to environmental or social justice issues, are an explicit outcome of community-based, community-driven, and participant action research projects (Wilderman et al. 2004; Cooper et al. 2007; Danielsen et al. 2009). And for the individual participant, personal fulfillment can include learning goals, the desire to contribute to science, or simply engaging in something enjoyable or fun (Raddick et al. 2010; Wright et al. 2015).

While we recognize the value of citizen science to both personal and societal outcomes, this paper explores strategies for better ensuring projects can meet declared goals based on scientific outcomes (i.e., optimizing project fitness to scientific purpose). Here we distinguish between the practice of science (including authentic science experiences on the part of the participants) and science outcomes (new information or knowledge, or applied work based on a scientific understanding of how the world works), where the latter must include the former, but the reverse is not the case. Our goal is to facilitate both acceptance and use of citizen science by the professional science community, and intentional design of projects with science as a primary objective. To that end, we: (1) present a science-focused typology that differentiates projects based on intent and activity; (2) define a process workflow to help identify design nexus points for science-focused projects; and (3) discuss quality control approaches to maximize data quality as a function of project scale and complexity.

A science-based typology of citizen science

Existing typologies of citizen science pivot on the degree to which participants are involved in tasks other than data collection. Bonney et al. (2009b) posited three points of project design along a continuum of interaction between scientist and participant. *Contributory* projects—also referred to as virtual and/or investigative projects (Wiggins and Crowston 2011), externally-driven monitoring with local data collectors (Danielsen et al. 2009), or distributed intelligence (Haklay 2013)—are designed by the mainstream science community with the role of data producer assigned to the public. At the other end of the continuum are co-created projects which involve participants in all stages of the scientific process, and are often associated with particular communities and specific concerns such as air or water quality, as in "extreme citizen science" or community-based participatory science focused on highly marginalized and often remote populations (Haklay 2013; Stevens et al. 2014). In fact, there are a range of projects which confer increasing power and project ownership to non-scientist participants including autonomous local monitoring (Danielsen et al. 2009), community-based participatory research (Wilderman et al. 2004), and more generally "action" projects (Wiggins and Crowston 2011). What often sets these projects apart is the explicit movement of project results into the sphere of decision-making and governance. In between these poles are collaborative projects expanding participants roles beyond data collector, from contributing to iterative versions of data collection protocols and training of new recruits, to results interpretation and defining the next phase(s) of the research (Cooper et al. 2007).

What is apparent about most of these typologies is that they are centered on the roles and degree of control accorded to professional scientists versus other participants. We suggest that a science-focused typology aimed at classifying projects according to their potential for inclusion in scientific research and science-based decision-making is also needed to guide the scientific community in identifying projects applicable to their work. In lieu of a meta-analysis systematically reviewing attributes of all citizen science projects (e.g., the 1800 projects currently listed in SciStarter.org), we generated our schema through an iterative process that extended a framework presented at the Waypoints of Science: Scaling Design, Development and Delivery of Citizen Science for Bonafide Science symposium held at the Citizen Science Association meeting in 2017. Iterations were tested against: (1) all projects (unique projects = 80) highlighted as examples in all previous literature proffering a typology or categorization of citizen science (i.e., see references above), (2) the 388 biodiversity citizen science projects collected in the Theobald et al. (2015) meta-analysis, (3) projects managed directly by the authors, and projects associated with and/or analogous to or duplicative of those projects (e.g., all projects focused on beach habitats; projects focused on documenting phenology), and (4) all projects on data collection platforms managed by the authors (e.g., in the Zooniverse). In total, over 500 projects were tested against our typology.

The right-hand branch of Fig. 1—no/minimal data—is defined by projects for which the primary intent is not data collection at a level or scale needed to address an issue or question of scientific interest. Education and awareness projects may well bring members of the public into direct contact with practicing scientists for the first time, and may provide individuals with authentic scientific experiences, without contributing to the advancement of science. Examples include the Lost Ladybug Project (Gardiner et al. 2012) which focuses on youth programs to identify native and invasive ladybugs, and the youth-focused intertidal project Long-term Monitoring Program and Experiential Training for Students, or LiMPETS (Ballard et al. 2017). In both of these examples, hundreds of middle school students annually gain authentic science experiences, become more aware of scientific practice and environmental issues, and may gain agency (permission to act) and expand their identity through participation (Ballard et al. 2017). However, standardized, effort-controlled, verifiable data at a spatio-temporal scale equivalent to questions of scientific interest are rarely produced. Non-data collection tasks include a broad swath of activities where participants may be deeply engaged in assistance toward a goal that does not require the collection or processing of information, as in conservation action and restoration projects (Bruyere and Rappe 2007).

The left-hand branch—data generated—separates out projects where the primary intent is the creation of information, or data in service of a scientific goal. We define "data" as an abstraction—a measurement, classification, and/or count that individually or collectively characterizes an object, phenomenon, or state—as well as the thing itself, as in a sample. First, we divide projects by whether the participant is directly engaged in thinking, or is giving tacit permission for the use of "information and communication technologies" (Wiggins and Crowston 2011). Passive participation ranges from computation, or the use of networked desktops and laptops to parallel process discrete "work packages" as part of big data projects (e.g., SETI@home, Rosetta@home, climateprediction.net), to sensing, defined as personally carrying and/or housing automated sensors which report data directly (e.g., Quake-Catcher Network, where participants host seismic sensors on their laptops; Cochran et al. 2009). Although science is clearly being accomplished in both cases, the

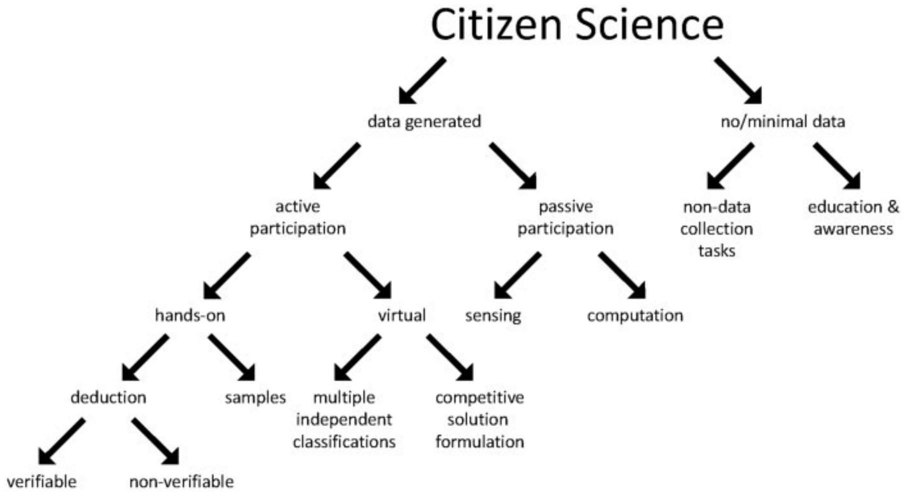


Fig. 1 A typology of citizen science separating projects according to scientific intent and participant activities. The first branching separates projects by primary goal: generation of science outcomes (e.g., data generated) or other goals (e.g., education, community empowerment, or personal fulfillment) for which data generation is possible but not necessary. Note any single branch point does not define mutually exclusive space (e.g., awareness/education is possible on the left side of the tree, and deduction can be accomplished virtually).

participant is passive in the sense of a non-thinking contribution which can be accomplished without specific understanding of how their participation contributes to science.

By contrast, active participation requires participants to engage directly in one or more of the tasks of the scientific process. Types of activity can be divided into physical hands-on work and virtual citizen science—where the latter is conducted entirely through a computer interface, often online, whether that is situated in a kiosk at a visitor's center or in a science museum, at home, or on a mobile device. Virtual citizen science capitalizes on crowdsourcing, a distributed production model that makes an open call for contributions from a large, undefined network of people (Howe 2006) to achieve both faster task accomplishment and higher project-wide accuracy with no precondition or expectation of long-term engagement.

Two basic approaches to crowdsourcing in service of science include: multiple independent classifications and competitive solution formulation. In the former, the accuracy of the individual participant is secondary to the "wisdom of the crowd" emerging through the use of voting or aggregation algorithms (Fortson et al. 2012). Advanced algorithms account for individual performance, assigning additional weight to responses from participants who are more accurate, and/or who contribute more (e.g., Marshall et al. 2016). Zooniverse—an online, crowdsource classification platform currently hosting ~80 projects is the exemplar. Zooniverse participants can choose to classify everything from camera-trapped mammals in East Africa (Snapshot Serengeti) to feather color from digital stills of museum specimens (Project Plumage) to leaves on growing plants (Leaf Targeting). By contrast, competitive solution formulation uses the crowd to find the single best participant, as in the protein structure game Foldit (Khatib et al. 2011) or the multiple sequence alignment game Phylo (Kawrykow et al. 2012). Task performance is tied directly to recognition and thus a degree of competition (e.g., Greenhill et al 2014), and the "game" may become relatively distinct from the underlying science.

Finally, hands-on citizen science is typified by a wide range of projects from laboratory-based work to field-based environmental science. These projects include both monitoring and experimental studies, all of which require physical collection of data. Sample collection includes direct contact with the sampled material, as in SoundCitizen, a water quality project requiring participants to send in water samples for laboratory analysis (Keil et al. 2011); and/or may simply be a geo-referenced, time-stamped photograph, as in CrowdWater, which collects hydrological data based on photographs (Seibert et al. 2017). In deduction, a decision is made based on the original data or evidence collected (e.g., species identification based on morphological characters), as in the fish identification dive program Reef Environmental Education Foundation Fish Survey Project (REEF; Thorson et al. 2014). For verifiable deductions, the decision reached by a participant can be independently verified; that is, an expert can evaluate the collected evidence, as is the case with Earthwatch, where experts are on-site with participants (Chandler et al. 2012). Non-verifiable deductions can still have high scientific value, especially when the volume or scale of data collected is high or large, as is the case for the Christmas Bird Count, or eBird (Sullivan et al. 2014). In virtual projects, verification solutions are implicit in the crowdsource approach.

Designing for science and citizen science

An increasing body of literature suggests that non-professional participants engaged in hands-on, deductive citizen science may underperform relative to professionals. For example, project participants tend to under-report common species and over-report rare species (Kremen et al. 2011; Paul et al. 2014). Participants over-report easy-to-identify, flashy, brightly colored or especially charismatic species (Ward 2014; Boakes et al. 2016) and under-report cryptic species (Cox et al. 2015). Non-professionals are less likely to master non-visual survey methods (e.g., acoustic surveys, scat surveys; Moyer-Horner et al. 2012), and are more likely to collect information non-systematically across the landscape (Boakes et al. 2016). In contrast, a meta-analysis of 509 ecological and environmental citizen science projects (Pocock et al. 2017) found that "best quality of data" was associated with in-person training, production of associated materials (e.g., a protocol), and the use of specialized equipment for data collection.

For citizen science to become an accepted form of bona-fide science, intentional design with attention to data quality is essential, including measures of quality assurance (the procedures to enhance data quality undertaken before and during data collection) and methods of quality control (the processes for improving quality after data collection). Burgess et al. (2017) found that biodiversity scientists overwhelmingly agreed on the following quality assurance measures for field-collected data: documentation of sampling location, time, and date; effort control via known area and/or time envelope of sampling; verifiable data; and data collection personnel trained by an expert.

We abstracted the scientific process as a series of steps (left side, Fig. 2) from project design through to publication and use, that can be understood as necessary in both science (flowchart in gray, Fig. 2) and citizen science (flowchart in white, Fig. 2). The design of any scientific project design involves the selection of a sampling scale and a level of precision for data collection that match the question or issue at hand, as well as selecting a minimum sample size (*N* floor) that addresses the variability inherent in the system. Once the data are collected, the post-processing step involves refining an analytic approach suited to the data and the question. The final step in science is presenting the work in a peer-reviewed publication.

Quality assurance in citizen science

Citizen science as a method of science is not different, but requires additional attention to aspects of quality assurance. During project design, intentional recruitment of target audiences can be key to success. Individuals are differentially attracted to projects based on personal values and shared goals (Evans et al. 2005; Rotman et al. 2012). Thus, making project goals explicit allows individuals who may have different, even antithetical, goals to consider whether their needs are being met, perhaps selecting another project more closely aligned to their own world-view. Attention to ability, or level of content knowledge and skill development as novice participants, is also essential. Projects are variably accessible relative to physical ability, economic status, and time available among other features (Pandya 2012). Whether recruits can accomplish the work will also vary as a function of their "distance" from the content and the complexity of the tasks (Jung et al. 2005; Kosmala et al. 2016). For instance, while some projects attract hobbyists with a high degree of skill and little need of formal training (e.g., birders, amateur astronomers—Jones et al. 2017a), many projects attract a broad swath of interested non-experts with little-to-no *a priori* training (Kelling et al. 2015).

Within the realm of citizen science, project development follows from the intersection of participant ability and the sampling precision required by the project, and includes two types of interaction with participants: training and participant-specific materials. While scientists prefer citizen science data collected by projects with in-person expert training (Burgess et al. 2017), online trainings can also be effective (Masters et al. 2016), and may be the only way to scale projects beyond local-to-regional geographies. Project materials include, at a minimum, a well-developed protocol outlining all of the steps needed to perform tasks successfully, and project-specific tools (e.g., measuring equipment, data sheets). Parrish et al. (2017) suggest serial refinement of project materials—(in this case, a field key to beached birds) by non-professional, non-experts in the target audience in collaboration with project

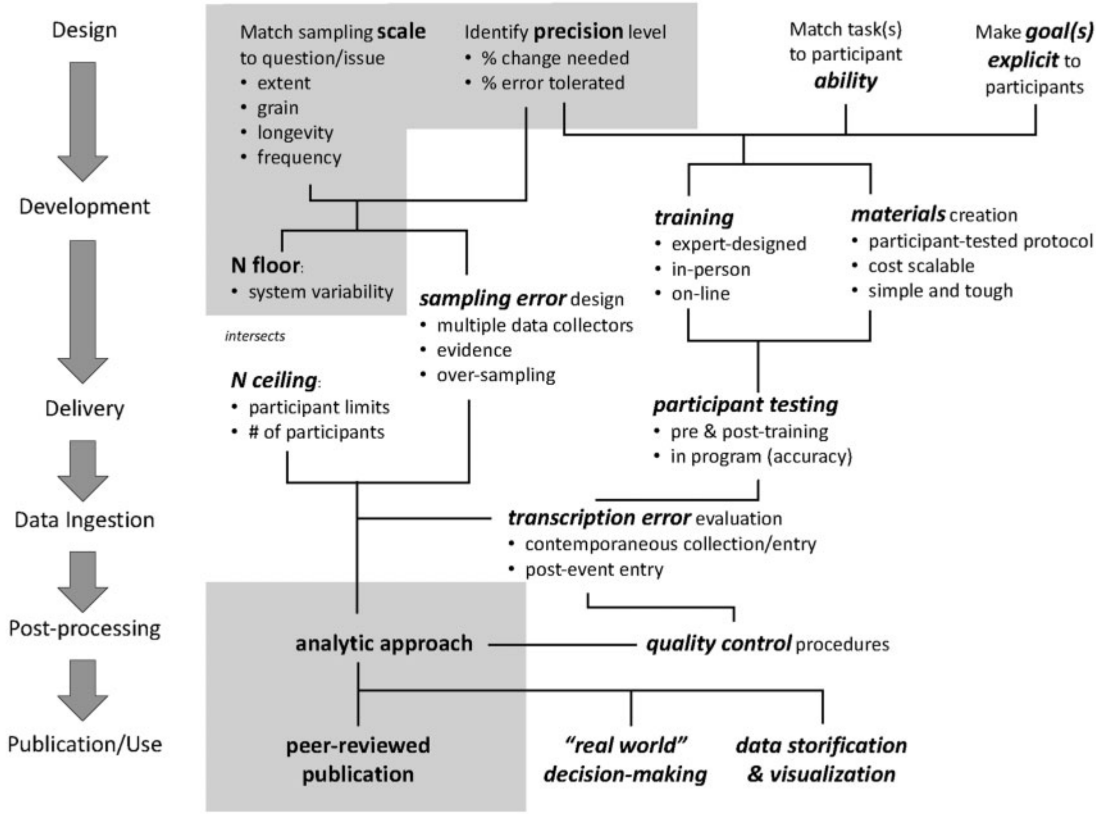


Fig. 2 The steps of science (listed sequentially at left) outlined as a flowchart. At each stage, the necessary elements inherent in all science projects are highlighted in bold print and encased within the gray box across stages. Additional elements specific to citizen science are highlighted in bold italics, and fall outside the gray box.

scientists—to identify and replace or explain jargon and otherwise clarify materials. Co-creation and/or refinement of the training, protocol, and associated data collection materials among scientists, project staff, and project participants can improve both data quality and participant retention (Kim et al. 2011). Attention to cost-effectiveness, including both the price of provided materials and their durability, is important because the scaled success of a project—recruiting thousands of participants—should not cause its financial failure nor exclude potential participants in disadvantaged circumstances.

In the delivery of the project, quality assurance can be affected through participant testing and attention to sampling. Testing participant knowledge can be used to ensure that trainings are successful in delivering both content and skill (e.g., pre-post testing surrounding a training), as well as to ensure continued quality as participants engage in the practice of project tasks; that is, do the work. For online image classification projects, inserting a certain proportion of images where the answer is already known can create an accuracy baseline for each participant. Such evaluation built directly into the normal flow of activities (i.e., embedded assessment) can also support timely feedback. For participants, understanding what they are doing incorrectly and how to correct it, as well as recognition of correctly accomplished tasks, can be empowering and lead to increased retention (Haywood et al. 2016). For project designers, understanding process breakdowns is essential for adaptively managing project training and materials to maximize data quality, as well as to understand the types and levels of error resulting from hundreds to thousands of data collectors. Although minimum sample size is set by system variability, maximum sample size (*N* ceiling) should be set relative to what individual participants can reasonably be expected to contribute, multiplied by the number of participants (minimally) in the program. Because citizen science is, by definition, the work of the many, attending to the sampling error inherent in this design is important, and may further increase sampling needs depending on whether participants are collecting deductive data that is (or isn't) backed up by evidence.

Data ingestion is automatic in some projects (e.g., all passive participation and some virtual, and sample collection projects) such that transcription error is non-existent. Virtual projects focused on classification (e.g., projects within the Zooniverse) minimize transcription error via the crowdsource design of multiple, independent classifiers for each task. However, hands-on projects may provide participants with the opportunity to input data they collect, introducing another source of error in the data. Mobile technologies may offer solutions by automatically logging some data (e.g., date, time, location, limited environmental data, and photographic evidence).

Quality control in citizen science

Within citizen science, post-processing prior to analysis offers many possibilities for *post-hoc* improvement to data via quality control procedures, even in cases where quality assurance has been relatively weak. In Fig. 3, we conceptualize citizen science projects from those featuring relatively simple tasks requiring little-to-no deductive reasoning on the part of the participant (e.g., collecting a water sample, collecting a photograph sample) to those requiring participants to engage in complicated work requiring advanced training, deductive reasoning, mastery through practice, and/or a mental model of the system (e.g., species identification, performing chemical analyses on water quality samples). Orthogonal to the axis of task complexity, we array projects as a function of scale, from local projects with relatively few participants to projects that span regions (e.g., large marine ecosystems, countries, or continents) up to—at least theoretically—the globe. While not completely interchangeable, projects with a larger geographic extent also tend to be those with higher participant numbers (Theobald et al. 2015). Virtual projects, which are effectively aspatial, can similarly scale in participant numbers and total tasks completed.

For simple tasks (left side of Fig. 3), data quality can be improved by "outsourcing" the thinking to scientists, that is, restricting citizen involvement to straightforward sample collection tasks while scientists receive, verify, catalog, and analyze the samples and the resulting data (i.e., do the thinking). In the case of virtual projects with numbers of participants (upper left quadrant of Fig. 3), data quality can be improved via crowdsourcing tasks to multiple individuals, with task completion automatically based on algorithm voting or consensus metrics (e.g., species identification projects on the Zooniverse platform). For example, Swanson et al. (2016) found that crowdsourced (>10 people classifying an image) identifications of images in Snapshot Serengeti were slightly (97.9%) more accurate than even expert identifications (96.6%). Algorithms can also identify individual players who are particularly adept, or inept, and assign coefficients accordingly (Hines et al. 2015), creating more accurate data (Marshall et al. 2016)—akin to statistical pruning. While outsourcing is constrained by scientific resource time to smaller projects, crowdsourcing supports very large projects with millions of images to be processed (e.g., Lintott et al. 2008). Here, even inaccurate answers can prove valuable information if a given participant's bias is systematic (Masters et al. 2016).

As task complexity increases at small project scales (lower right quadrant of Fig. 3), options for quality control shift toward expert intervention. On-site expert facilitation and mentoring is exemplified by Earthwatch where scientists train, mentor, and remain on-site with participants throughout the tenure of the project (Chandler et al. 2017). In independent record verification, participants' deductions are subsequently verified via photographs or specimens. For example, in the COASST program all species identifications (marine birds) are independently verified by experts via participant-collected primary evidence (foot type, standardized measurements, scaled dorsal, and ventral photographs), a process that improves identification to species level from 83% (participant rate) to 92% (Parrish et al. 2017). Verification can also proceed at the local phenomenological level, as in tracking the invasion front of the Asian tiger mosquito (*Aedes albopictus*) in Spain, where participant reports via the Mosquito Alert app were independently verified via ovitrapping (Palmer et al. 2017).

As project scales increase to continental and beyond (upper right quadrant of Fig. 3), quality control of individual data points may be less practical as volume prohibits comprehensive expert review, but statistical pruning, flagging, and other *post hoc* techniques can weed out anomalous data points (e.g., mixed effect models and machine learning: Bird et al. 2014; false-positive occupancy models: Pillay et al. 2014), or computational models can be used to create smoothed, interpolated versions of the original data (e.g., spatiotemporal exploratory models: Hochachka et al. 2012). In between, participant profiling (e.g., trust metrics: Hunter et al. 2013; occupancy-detection-experience model: Hochachka et al. 2012) can be used to winnow or weight data based on participants' known performance levels; however, this approach can introduce difficult decisions about the ethics of selective data use.

Use beyond science

For most academics, the ultimate step is dissemination of results into the scientific literature (i.e.,

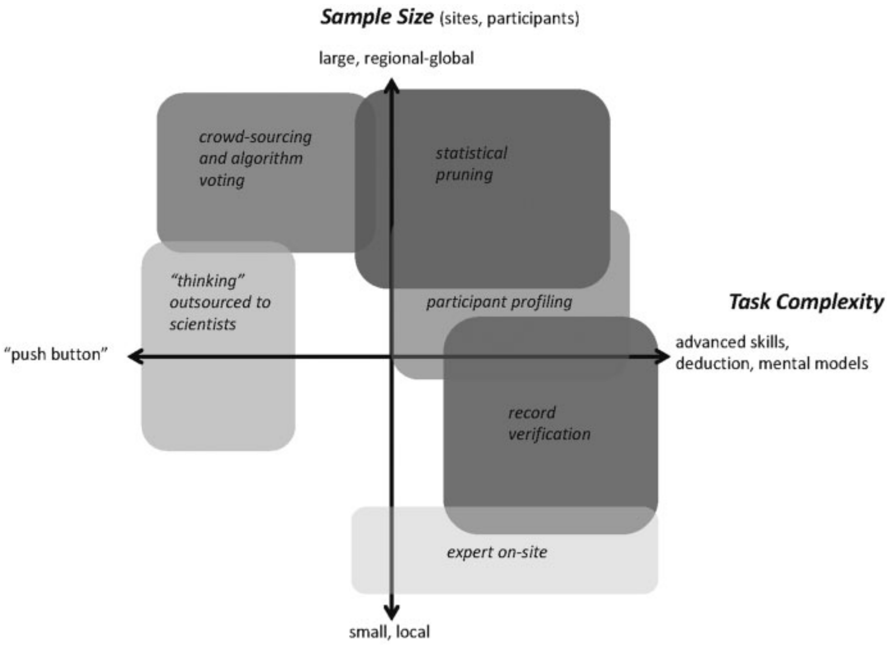


Fig. 3 Approaches to quality control in citizen science as a function of the scale and complexity of the task(s) performed by participants. Shading is used to visually highlight the different approaches. Regions of overlap indicate intersections of task complexity and sample size within which multiple solutions might be found.

"publication/use" step in Fig. 2), simultaneously validating the work through review by scientific peers while daylighting the work to the larger scientific community. However, long-term maintenance of a citizen science project requires two additional and on-going steps: demonstrating that science is applied as promised, and sharing the results with participants (Cox et al. 2015). For some projects, taking results directly into "real world" decision-making processes (e.g., conservation, resource management) is the social contract that contributors make as a precondition for participation (Haywood et al. 2016). For place-based, environmental justice projects, such decision-making is the primary, even exclusive, goal (Haklay 2013).

Finally, returning "results-at-scale" to participants in suitable text and graphical forms (i.e., data storification and visualization, Fig. 2) can be essential to participant retention (Cox et al. 2015). Species migration (e.g., eBird—Sullivan et al. 2014), the timing of spring flowering (e.g., National Phenology Network—Rosemartin et al. 2014), the occurrence and location of extreme weather (e.g., CoCoRaHS—Gochis et al. 2015), the spread of disease across a population (e.g., Sea Star Wasting—Montecino-Latorre et al. 2016), the extent of a marine bird mass mortality event (e.g., COASST—Jones et al. 2017b)—these "data stories" are all patterns that transcend the ability of a single participant to directly observe the emergent pattern. Without these stories, participants cannot "see" their own data as contributing to the greater whole, and may be unaware of actual data uses. With these stories, participants refer to the work as "purposeful and powerful" and may be energized to take action, from continued engagement to calling for conservation stewardship or other resource management outcomes (Haywood et al. 2016).

Conclusions

Citizen science progresses through the actions of the many. The collective work of hundreds to hundreds-of-thousands creates datasets that bound phenomena and address issues of scientific and management interest at spatio-temporal scales otherwise unattainable (Theobald et al. 2015). With this promise comes responsibility:

- from the scientific community to erase or at least understand bias and to embrace well-designed, scale-, and content-appropriate projects as a valid source of information;
- from project designers to attend to the specifics of quality assurance and quality control needed to produce rigorous, high quality data, if science is the primary goal;
- from project owners and managers to honestly advertise the type of project, depth of participant

engagement, and quality and limitations of project data, and to ensure fitness to declared purpose;

- from participating scientists to follow through on data use and data stories providing both the scientific community and the participant corps and their communities with results-at-scale;
- and from participants to choose projects wisely according to their values and goals, to contribute as much and as well as they can, and to hold project managers to their declarations of purpose or intent.

Without judgment, we suggest the use of a science-based typology to sort existing projects will increase the "honest signaling" needed to help the mainstream science community see and understand citizen science as a bonafide method for generating legitimate scientific outcomes. Furthermore, the degree to which the individual participant: (1) understands and values the precision and accuracy required of the task(s) they are performing; (2) applies "thinking" skills requiring mastery of simple tasks to successfully perform more complex ones (e.g., species identification); and (3) can literally "see" their work (data collection or otherwise) within the larger context defined by the science at scale, will structure their degree of engagement and will impact data quality. Because task performance is often dependent on accrued experience within a project (Kelling et al. 2015; Kosmala et al. 2016), the strategies we have outlined herein (i.e., Fig. 2) support the "learning curve" and improve retention by providing transparency about project goals and data quality processes that match fitness to purpose (Juran 1951).

Pocock et al. (2017) found that the recent 10% per annum growth rate in ecological and environmental citizen science has primarily been realized through online projects with mass, often short-term, participation in low-complexity data collection. Growth in field-based, hands-on approaches is more difficult, but can return data on global change impacts from climate to disease to invasions and ecosystem change (Theobald et al. 2015). Thus, we argue that both approaches—simplification at scale, and complexity with care—are valid and valuable strategies for citizen science projects to generate rigorous and robust science outcomes.

Acknowledgments

Contribution to the dedicated SICB volume on "*Science in the Public Eye*" January 2018 meeting symposium. Portions of this manuscript were conceived at a citizen science workshop sponsored by the US Department of Agriculture-Forest Service and Schoodic Institute. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

Funding

A.W. was supported in part by U.S. Geological Survey (USGS) Cooperative Agreement G16AC00267 and National Science Foundation (NSF) grant 0830944. J.K.P. and H.B. were partially supported by NSF EHR/DRL awards 1114734 and 1322820, and Washington Sea Grant award R/OLWD-1. B.S. acknowledges support from the National Aeronautics and Space Administration (NASA) through Einstein Postdoctoral Fellowship Award Number PF5-160143 issued by the Chandra X-ray Observatory Center, which is operated by the Smithsonian Astrophysical Observatory for and on behalf of NASA under contract NAS8-03060. L.F. acknowledges partial support from NSF IIS 1619177.

References

Ballard HL, Dixon CGH, Harris EM. 2017. Youth-focused citizen science: examining the role of environmental science learning and agency for conservation. Biol Conserv 208:65–75.

Bird TJ, Bates AE, Lefcheck JS, Hill NA, Thomson RJ, Edgar GJ, Stuart-Smith RD, Wotherspoon S, Krkosek M, Stuart-Smith JF. 2014. Statistical solutions for error and bias in global citizen science datasets. Biol Conserv 173:144–54.

Boakes EH, Gliozzo G, Seymour V, Harvey M, Smith C, Roy DB, Haklay M. 2016. Patterns of contribution to citizen science biodiversity projects increase understanding of volunteers' recording behaviour. Sci Rep 6:33051.

Bonney R, Cooper CB, Dickinson J, Kelling S, Phillips TB, Rosenberg KV, Shirk J. 2009a. Citizen science: a developing tool for expanding science knowledge and scientific literacy. BioScience 59:977–84.

Bonney R, Ballard H, Jordan H, McCallie E, Phillips T, Shirk J, Wilderman C. 2009b. Public participation in scientific research: defining the field and assessing its potential for informal science education. A CAISE Inquiry Group Report. Washington, DC: Center for Advancement of Informal Science Education (CAISE).

Bovy KM, Watson JE, Dolliver J, Parrish JK. 2016. Distinguishing offshore bird hunting from beach scavenging in archaeological contexts: the value of modern beach surveys. J Archaeol Sci 70:35–47.

Bruyere B, Rappe S. 2007. Identifying the motivations of environmental volunteers. J Environ Plann Manage 50:503–16.

Burgess H, DeBey LB, Froehlich H, Schmidt N, Theobald EJ, Ettinger AK, HilleRisLambers J, Tewksbury J, Parrish JK. 2017. The science of citizen science: exploring barriers to use as a primary research tool. Biol Conserv 208:113–20.

Chandler M, Bebber DP, Castro S, Lowman MD, Muoria P, Oguge N, Rubenstein DI. 2012. International citizen science: making the local global. Front Ecol Environ 10:328–31.

Chandler M, Rullman S, Cousins J, Esmail N, Begin E, Venicx G, Eisenberg C, Studer M. 2017. Contributions to publications and management plans from 7 years of citizen science: use of a novel tool on Earthwatch-supported projects. Biol Conserv 208:163–73.

Cochran ES, Lawrence JF, Christensen C, Jakka RS. 2009. The quake-catcher network: citizen science expanding seismic horizons. Seismol Res Lett 80:26–30.

Cooper CB, Dickinson J, Phillips T, Bonney R. 2007. Citizen science as a tool for conservation in residential ecosystems. Ecol Soc 12:11–22.

Cooper CB, Shir J, Zuckerberg B. 2014. The invisible prevalence of citizen science in global research: migratory birds and climate change. PLoS One 9:e106508.

Cox J, Oh EY, Simmons B, Lintott C, Masters K, Graham G, Greenhill A, Holmes K. 2015. Defining and measuring success in online citizen science: a case study of zooniverse projects. Comput Sci Eng 17:28–41.

Danielsen F, Burgess N, Balmford A, Donald P, Funder M, Jones J, Alviola P, Balete D, Blomley T, Brashares J, et al. 2009. Local participation in natural resource monitoring: a characterization of approaches. Conserv Biol 23:31–42.

Dickinson JL, Zuckerberg B, Bonter DN. 2010. Citizen science as an ecological research tool: challenges and benefits. Annu Rev Ecol Evol Syst 41:149–72.

Eiben CB, Siegel JB, Bale JB, Cooper S, Khatib F, Shen BW, Players F, Stoddard BL, Popovic Z, Baker D. 2012. Increased diels-alderase activity through backbone remodeling guided by Foldit players. Nat Biotechnol 30:190–2.

Evans C, Abrams E, Reitsma R, Roux K, Salmonsen L, Marra PP. 2005. The neighborhood nestwatch program: participant outcomes of a citizen-science ecological research project. Conserv Biol 19:589–94.

Fortson LF, Masters K, Nichol R, Borne K, Edmondson EM, Lintott C, Raddick J, Schawinski K, Wallin J. 2012. Galaxy zoo: morphological classification and citizen science. In: Way MJ, Scargle JD, Ali KM, Srivastava AN, editors. Advances in machine learning and data mining for astronomy. Boca Raton (FL): CRC Press, Taylor & Francis Group. p. 213–36.

Gardiner MM, Allee LL, Brown PMJ, Losey JE, Roy HE, Smyth RR. 2012. Lessons from lady beetles: accuracy of monitoring data from US and UK citizen-science programs. Front Ecol Environ 10:471–6.

Gochis D, Schumacher R, Friedrich K, Doesken N, Kelsch M, Sun J, Ikeda K, Lindsey D, Wood A, Dolan B. 2015. The great Colorado flood of September 2013. Bull Am Meterol Soc 96:1461–87.

Goodchild M. 2007. Citizens as sensors: the world of volunteered geography. GeoJournal 69:211–21.

Greenhill A, Holmes K, Lintott C, Simmons B, Masters K, Cox J, Graham G. 2014. Playing with science: gamised aspects of gamification found on the Online Citizen Science Project—Zooniverse. In: Dickinson P, editor. GAMEON 2014. Lincoln: EUROSIS—The European Multidisciplinary Society for Modelling and Simulation Technology. p. 15–24.

Haklay M. 2013. Citizen science and volunteered geographic information: overview and typology of participation. In: Sui DZ, Elwood S, Goodchild MF, editors. Crowdsourcing geographic knowledge: voluteered geographic information (VGI) in theory and practice. Berlin: Springer. p. 105–22.

Hays GC, Richardson AJ, Robinson C. 2005. Climate change and marine plankton. Trends Ecol Evol 20:337–44.

Haywood B, Parrish JK, Dolliver J. 2016. Place-based, data-rich citizen science as a precursor for conservation action. Conserv Biol 30:476–86.

Hines G, Kosmala M, Swanson A, Lintott CJ. 2015. Aggregating user input in ecology citizen science projects. Proceedings of the Twenty-Seventh Conference on Innovative Applications of Artificial Intelligence. Palo Alto (CA): AAAI Press. p. 3975–80.

Hochachka WM, Fink D, Hutchinson RA, Sheldon D, Wong WK, Kelling S. 2012. Data-intensive science applied to broad-scale citizen science. Trends Ecol Evol 27:130–7.

Howe J. 2006. The rise of crowdsourcing. Wired Magazine, June 2006.

Hunter J, Alabri A, van Ingen C. 2013. Assessing the quality and trustworthiness of citizen science data. Concurr Comput 25:454–66.

Irwin A. 1995. Citizen science: a study of people, expertise, and sustainable development. New York (NY): Routledge.

Jones MG, Corin EN, Andre T, Childers GM, Stevens V. 2017a. Factors contributing to lifelong science learning: amateur astronomers and birders. J Res Sci Teach 54:412–33.

Jones TJ, Parrish JK, Punt AE, Trainer VL, Kudela R, Lang J, Brancato MS, Odell A, Hickey B. 2017b. A mass mortality event of marine birds in the Northeast Pacific caused by *Akashiwo sanguinea*. Mar Ecol Progr Ser 579:111–27.

Jones TJ, Parrish JK, Peterson WT, Bjorkstedt EP, Bond NA, Ballance LT, Bowes V, Hipfner JM, Burgess HK, Dolliver JE, et al. 2018. Massive mortality of a planktivorous seabird in response to a marine heatwave. Geophys Res Lett 45:3193–202.

Jung W, Olfman L, Ryan T, Park YT. 2005. An experimental study of the effects of contextual data quality and task complexity on decision performance. Proceedings of the IRI—2005 IEEE International Conference on Information Reuse and Integration. IEEE. p. 149–54.

Juran JM, (ed.). 1951. Quality-control handbook. 1st ed. New York (NY): McGraw-Hilll.

Kawrykow A, Roumanis G, Kam A, Kwak D, Leung C, Wu C, Zarour E, Sarmenta L, Blanchette M, Waldispühl J. 2012. Phylo: a citizen science approach for improving multiple sequence alignment. PLoS One 7:e31362.

Keil R, Salemme K, Forrest B, Neibauer J, Logsdon M. 2011. Differential presence of anthropogenic compounds dissolved in the marine waer of Puget Sounds, WA and Barkley Sound, BC. Mar Pollut Bull 62:2404–11.

Kelling S, Johnston A, Hochachka WM, Iliff M, Fink D, Gerbracht J, Lagoze C, La Sorte FA, Moore T, Wiggins A. 2015. Can observation skills of citizen scientists be estimated using species accumulation curves?. PLoS One 10:e0139600.

Khatib F, Cooper S, Tyka MD, Xu K, Makedon I, Popovic Z, Baker D, Players F. 2011. Algorithm discovers b protein folding game players. Proc Natl Acad Sci U S A 108:18949–53.

Kim S, Robson C, Zimmerman T, Pierce J, Haber EM. 2011. Creek watch: pairing usefulness and usability for successful citizen science. Proceedings of the SIGCHI Conference on Human Factors in Computing Systems (CHI '11). New York (NY): ACM. p. 2125–34.

Kosmala M, Wiggins A, Swanson A, Simmons B. 2016. Assessing data quality in citizen science. Front Ecol Environ 14:551–60.

Kremen C, Ullman KS, Thorp RW. 2011. Evaluating the quality of citizen-scientist data on pollinator communities. Conserv Biol 25:607–17.

Lintott CJ, Schawinski K, Slosar A, Land K, Bamford S, Thomas D, Raddick MJ, Nichol RC, Szalay A, Andreescu D, et al. 2008. Galaxy zoo: morphologies derived from visual inspection of galaxies from the Sloan Digital Sky Survey. Mon Not R Astron Soc 389:1179–89.

Marshall PJ, Verma A, More A, Davis CP, More S, Kapadia A, Parrish M, Snyder C, Wilcox J, Baeten E, et al. 2016. SPACE WARPS—I. Crowdsourcing the discovery of gravitational lenses. Mon Not R Astron Soc 455:1171–90.

Masters K, Oh EY, Cox J, Simmons B, Lintott C, Graham G, Greenhill A, Holmes K. 2016. Science learning via participation in online citizen science. J Sci Commun 15:A07.

Montecino-Latorre D, Eisenlord ME, Turner M, Yoshioka R, Harvell CD, Pattengill-Semmens CV, Nichols JD, Gaydos JK. 2016. Devastating transboundary impacts of sea star wasting disese on subtidal asteriods. PLoS One 11:e0163190.

Moyer-Horner L, Smith MM, Belt J. 2012. Citizen science and onserver variability during American pika surveys. J Wildl Manage 76:1472–9.

Palmer JRB, Oltra A, Collantes F, Delgado JA, Lucientes J, Delacour S, Bengoa M, Eritja R, Bartumeus F. 2017. Citizen science provides a reliable and scalable tool to track disease-carrying mosquitoes. Nat Commun 8:916–29.

Pandya R. 2012. A framework for engaging diverse communities in citizen science in the US. Front Ecol Environ 10:314–7.

Parrish JK, Litle K, Dolliver J, Hass T, Burgess H, Frost E, Wright C, Jones T. 2017. Defining the baseline and tracking change in seabird populations: the Coastal Observation and Seabird Survey Team (COASST). 2017. In: Cigliano JA, Ballard HL, editors. Citizen science for coastal and marine conservation. New York (NY): Routledge. p. 19–38.

Paul K, Quinn MS, Huijser MP, Graham J, Broberg L. 2014. An evaluation of a citizen science data collection program for recording wildlife observations along a highway. J Environ Manage 139:180–7.

Pillay R, Miller WAW, Hines JE, Joshi AA, Madhusudan MD. 2014. Accounting for false positives improves estimates of occupancy from key informant interviews. Divers Distrib 20:223–35.

Pocock MJO, Tweddle JC, Savage J, Robinson LD, Roy HE. 2017. The diversity and evolution of ecological and environmental citizen science. PLoS One 12:e0172579.

Powell J, Nash G, Bell P. 2013. GeoExposures: documenting temporary geological exposures in Great Britain through a citizen-science website. Proc Geol Assoc 124:638–47.

Raddick MJ, Bracey G, Gay PL, Lintott CJ, Murray P, Schawinski K, Szalay AS, Vandenbert J. 2010. Galaxy zoo: exploring the motivations of citizen science volunteers. Astron Educ Rev 9:010103.

Riesch H, Potter C. 2014. Citizen science as seen by scientists: methodological, epistemological and ethical dimensions. Public Underst Sci 23:107–20.

Rosemartin AH, Crimmins TM, Enquist CAF, Gerst KL, Kellermann JL, Posthumus EE, Denny EG, Guertin P, Marsh L, Weltzin JF. 2014. Organizing phenological data resources to inform natural resource conservation. Biol Conserv 173:90–7.

Rotman D, Preece J, Hammock J, Procita K, Hansen D, Parr C, Lewis D, Jacobs D. 2012. Dynamic changes in motivation in collaborative citizen-science projects. Proceedings of the ACM 2012 Conference on Computer Supported Cooperative Work (CSCW '12). New York (NY): ACM. p. 217–226.

Seibert J, Etter S, Strobl B, Vis M, van Meerveld HJ. 2017. Can citizens observe what models need?—Evaluation of the potential value of crowd-based hydrological observations. 19th EGU General Assembly Conference Abstracts, Proceedings from the Conference held 23–28 April, 2017 in Vienna, Austria. p. 11620.

Stevens M, Vitos M, Altenbuchner J, Conquest G, Lewis J, Haklay M. 2014. Taking participatory citizen science to extremes. IEEE Pervasive Comput 13:20–9.

Sullivan BL, Aycrigg JL, Barry JH, Bonney RE, Bruns N, Cooper CB, Damoulas T, Dhondt AA, Dietterich T, Farnsworth A, et al. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. Biol Conserv 169:31–40.

Swanson A, Kosmala M, Lintott C, Packer C. 2016. A generalized approach for producing, quantifying, and validating citizen science data from wildlife images. Conserv Biol 30:520–31.

Theobald EJ, Ettinger AK, Burgess HK, DeBey LB, Schmidt NR, Froehlich HE, Wagner C, HilleRisLambers J, Tewksbury J, Harsch MA, et al. 2015. Global change and local solutions: tapping the unrealized potential of citizen science for biodiversity research. Biol Conserv 181:236–44.

Thorson JT, Scheuerell MD, Semmens BX, Pattengill-Semmens CV. 2014. Demographic modeling of citizen sciene data informs habitat preferences and population dynamics of recovering fishes. Ecology 95:3251–8.

Ward DF. 2014. Understanding sampling and taxonomic biases recorded by citizen scientists. J Insect Conserv 18:753–6.

Wiggins A, Crowston K. 2011. From conservation to crowdsourcing: a typology of citizen science. Proceedings of the Forty-Fourth Hawaii International Conference on System Science (HICSS-44), Koloa, HI. IEEE.

Wiggins A, Bonney R, LeBuhn G, Parrish JK, Weltzin J. 2018. A science products inventory for citizen-science planning and evaluation. BioScience 68:436–44.

Wilderman CC, Barron A, Imgrund L. 2004. From the field: service provider's experience with two operational models for community science. Community-Based Collaboratives Research Consortium Journal. Spring 2004.

Wright DR, Underhill LG, Keene M, Knight AT. 2015. Understanding the motivations and satisfactions of volunteers to improve the effectiveness of citizen science programs. Soc Nat Resour 28:1013–29.

Integrative and Comparative Biology

Integrative and Comparative Biology, volume 58, number 1, p. 161

Society for Integrative and Comparative Biology

Errata

Integrative and Comparative Biology; doi:10.1093/icb/icx073.

In the original, online publication of “Predicting Life-History Trade-Offs with Whole-Organism Performance,” by Simon P. Lailvaux and Dr. Jerry F. Husak, the incorrect PDF was published. The correct PDF is now associated with the article, and the corrected PDF is published in *Integrative and Comparatvie Biology*, Volume 57, Issue 2.

The publisher regrets this error.

doi:10.1093/icb/icx124

Advance Access publication January 2, 2018

Integrative and Comparative Biology; doi:10.1093/icb/icx053.

In the original, online publication of “Attention and Motivated Response to Simulated Male Advertisement Call Activates Forebrain Dopaminergic and Social Decision-Making Network Nuclei in Female Midshipman Fish,” by Dr. Paul Forlano et. al., the title incorrectly read “Attention and Simulated Motivated Response to Male Advertisement Call Activates Forebrain Dopaminergic and Social Decision-Making Network Nuclei in Female Midshipman Fish.” The title has now been corrected and the corrected manuscript is published in *Integrative and Comparatvie Biology*, Volume 57, Issue 4.

The publisher regrets this error.

doi:10.1093/icb/icx110

Advance Access publication October 23, 2017

2018 Membership Application / Dues Renewal

New Member or Member ID # ______________

Name: (First) ______________________ (Last) ______________________

Institution: ______________________ Dept: ______________________

Address (for confirmation): ______________________________________

____

City: ______________________ State/Country: ____________ Zip/Postal Code: ____________

Business Phone: ______________________ FAX: ______________________

Email: ______________________ Home Phone: ______________________

URL for your Web Page: ______________________________________

MEMBERSHIP OPTIONS

Annual Dues (Apr 1, 2018 - Mar 31, 2019)

Please check the appropriate category below. SICB is committed to conservation, and provides the journal electronically unless you opt here ☐ for hard copies.

☐ **FM** Full Member $105
☐ **FH** Full Member Family $145
☐ **EG** Emeritus $65
☐ **LM** Life Full Member $3,000
☐ **LM** Life Full Member Family $4,000
☐ 20 year Full Member $1,500
☐ 20 year Full Member Family $2,000
☐ **SS** Student $41
  ☐ High School Student
  ☐ Undergraduate Student
  ☐ Graduate Student
☐ **SF** Graduate Student Family $64
☐ **SP** Postdoctoral $50
☐ **FP** Postdoctoral Family $65

DIVISION AFFILIATION

From the eleven listed below, you may choose your divisional affiliation(s) with a checkmark:

☐ **DAB** Animal Behavior
☐ **DEE** Ecology & Evolution
☐ **DCB** Comparative Biomechanics
☐ **DEDE** Ecoimmunology and Disease Ecology
☐ **DCE** Comparative Endocrinology ($10 dues)
☐ **DIZ** Invertebrate Zoology
☐ **DCPB** Comparative Physiology & Biochem ($5 dues)
☐ **DNNSB** Neurobiology, Neuroethology, and Sensory Biology
☐ **DEDB** Evolutionary Developmental Biology
☐ **DPCB** Phylogenetics & Comparative Biology (formerly DSEB)
☐ **DVM** Vertebrate Morph ($5 students/postdocs) ($10 dues)

CONTRIBUTIONS

Please consider contributing to any of the following:

George A. Bartholomew Fund	$ _____
Howard A. Bern Lecture Fund	$ _____
Dwight Davis Fund	$ _____
Carl Gans Award Fund	$ _____
Libbie H. Hyman Memorial Scholarship Fund	$ _____
Charlotte Mangum Student Support Fund	$ _____
John A. Moore Lectureship Fund	$ _____
C. Ladd Prosser Symposium Fund	$ _____
Dorothy Skinner Memorial Award Fund	$ _____
Grants-in-Aid of Research/FGST	$ _____
Symposium Support Fund	$ _____
TOTAL Payment	**$**_________

DEMOGRAPHICS (Optional)

SICB has adopted the NSF categories to collect demographic information.

Gender: ☐ Male ☐ Female

Ethnicity (choose one):
☐ Hispanic or Latino, ☐ Not Hispanic or Latino,
☐ American Indian or Alaska Native, ☐ Asian,
☐ Black or African American,
☐ Native Hawaiin or Other Pacific Islander, ☐ White

Disability Status:
☐ Hearing Impairment, ☐ Visual Impairment,
☐ Mobility/Orthopedic Impairment, ☐ Other, ☐ None

Citizenship:
☐ US Citizen, ☐ US Permanent Resident,
☐ Other-Non US Resident

PAYMENT OPTIONS

Mail Check Payment to: SICB, 1313 Dolley Madison Blvd., Suite 402, McLean, VA 22101 or Fax to: (703) 790-2672

☐ VISA ☐ MasterCard ☐ American Express

Card # ______________________________________

Exp. Date ____________________ CV2# ____________________

Cardholder Name ______________________________________

Signature ______________________________________

Cardholder Billing Address ______________________________________

City ____________________ State ______ Zip ____________

Cardholder Phone ________________ Email ____________________

Refunds are not issued for purchase of Society for Integrative and Comparative Biology membership; membership is canceled when the membership term expires or if an individual requests that the membership be terminated.